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WITH SEVEN PLATES, AND NUMEROUS FIGURES IN THE TEXT

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ORIGINAL PAPERS PAGE

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STUDIES IN THE ECOLOGY OF BRECKLAND

III. THE ORIGIN AND DEVELOPMENT OF THE *FESTUCO-AGROSTIDETUM* ON ERODED SAND

BY A. S. WATT

(*With six Figures in the Text*)

CONTENTS

THE AREA INVESTIGATED

THE exposure of new soil over quite considerable areas is the result of wind erosion, often in the form of blow-outs, following degeneration of the vegetation (Watt, 1937). The building up of a new vegetation on this raw soil is the subject of this paper. In its major outlines the story is straightforward and simple enough; humus accumulates in the soil, simpler life-form dominants give way to higher, the plant communities become more complex and a relatively stable phase is eventually reached. In details the story is complex. While the vegetation as a whole moves up the inclined plane of seral development, different stages behave like the snail in the classic problem by constantly

slipping back from the position they have won, the surviving components starting afresh from a new position. Thus phases of building up and breaking down exist side by side forming cycles or waves of change in time and a patchwork in space of a most bewildering kind. And the phenomena are the more difficult to interpret because from first to last the actors in this drama are almost the same throughout. Lichens predominate, the soil is exceedingly infertile and the few higher plants—*Festuca ovina*, *Agrostis alba* and *A. tenuis* are the chief—living near subsistence level show a fairly lively response to changes in the climatic environment. From the experience gained one can now say that the whole study ought to have been carried out in one year or at any rate during a period of uniform climate. Actually the work was spread over 4 years, but the bulk of the data was obtained in 1933 and 1934, that is during the early and middle stages of the drought of 1933–35, and some gaps in the data could not be filled by a later appeal to the vegetation because of significant changes due to the drought.

The area investigated lies in the south-west corner of Lakenheath Warren on the threshold of the large blow-out at the place marked *X* in Fig. 9 of No. II of these studies (Watt, 1937). Here there is a complex of blow-outs in different stages of development, from a young blow-out the bottom of whose trough has not yet attained stability to old and broad dead blow-outs where the vegetation has reached the medial stages in development. At this place no later stages are found, but in its neighbourhood just across the road to the east and on the same soil both medial and late stages occur.

The whole area is grazed by rabbits.

The soil profile

The soil is an infertile sand 4–5 ft. (1·2–1·5 m.) deep overlying chalky boulder clay. Occasional subterranean peaks of this chalky boulder clay rise towards the surface and affect the vegetation locally but these variations are not dealt with.

The profile exposed in four pits dug in different stages of the sere reveals essentially the same features—a truncated sandy brown forest soil (brown earth) capped by an erosion pavement[1] or gravel layer exposed at the surface or covered by a thin layer of blown sand. The profile in the late stage of the sere is figured (Fig. 1) and described.

	cm.	
(1)	0–5	Blown sand darkened by humus
(2)	5–12	Sand with numerous flints (erosion pavement)
(3)	12–52	Rich fawn-red sand with few small scattered flints
(4)	52–100	As (3) but lighter in colour and showing horizontal narrow red-brown bands with a higher sesquioxide content
(5)	100–120	As (4) with the addition of small pea-sized sticky red-brown lumps
(6)	120–125	Rich red-brown sticky sand
(7)	125–	Chalky boulder clay

[1] I.e. a stony layer left behind by removal through erosion of finer material.

Samples of the different layers have been analysed mechanically and the data will be given and compared with other sets in a later communication on the soils of Breckland. For the present purpose it is enough to say that the soil is a sand, the "coarse sand" and "fine sand" fractions amounting, in each of the layers 1–5, to 93% or more. Silt and clay are negligible. That truncation of the soil profile, and in this particular profile burial under blown sand has occurred may be seen from the fractions got by passing the soil samples through a graduated series of sieves (Table I). Layer 2 is the "erosion pavement" with stones above 3 mm. in diameter accounting for 18% of the total—a much higher value than in any other layer. Most of the sand grains are less than 0·5 mm. in diameter: but 83% of these fine particles in the surface blown sand is a lower value than would be expected, due no doubt to the thinness of the layer and to contamination in sampling from the erosion pavement below. The soil is devoid of $CaCO_3$ (layers 1–5) and the surface layer is extremely acid (pH 4·2).

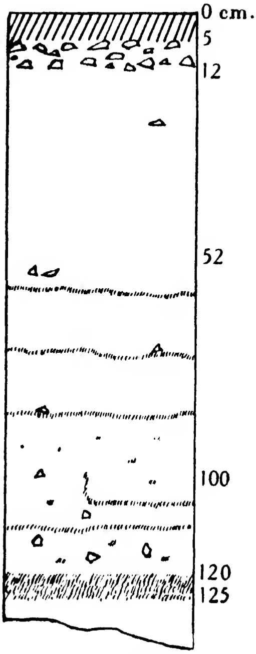


FIG. 1. Soil profile. For description see text, p. 2.

Table I. *Soil graded by sieving into fractions expressed as percentages of the total air-dry soil*

Soil layer ...	1	2	3	4	5
>3 mm.	1·17	18·33	0·59	0·31	6·09
2–3 mm.	0·92	1·91	0·23	0·12	0·44
1–2 mm.	5·90	6·05	0·45	0·47	2·55
0·5–1 mm.	8·84	5·91	1·64	1·65	5·57
<0·5 mm.	83·17	67·80	97·10	97·46	85·35

SOIL SAMPLING AND THE FACTORS DETERMINED

A fairly wide experience of Breckland has convinced me of the high sensitivity of the vegetation to variation in the superficial layers of sandy soils. This is particularly true of the lichen communities and to some degree also of the higher plants. To throw light on the behaviour of the lower plants in the succession samples of the superficial layer half an inch (1·3 cm.) in depth and approximately of the same volume were collected from each of the plots in each community. The total from each community was thoroughly mixed and provided the material for grading into fractions by sieving, for the determination of the organic matter (loss on ignition) and for the pH value (by Kuhn's colorimetric method). The estimation of the pH and humus was carried out on the fraction passing the 0·5 mm. sieve. Surface flints, important in

certain stages, were not included in the sample. The depth of the blown sand overlying the erosion pavement is also recorded.

General outline of the succession

The three major parts into which the sere is divided are called the Early, Middle and Late stages respectively. The Early stages comprise a series in which bare eroded soil is succeeded by plant communities in which lower

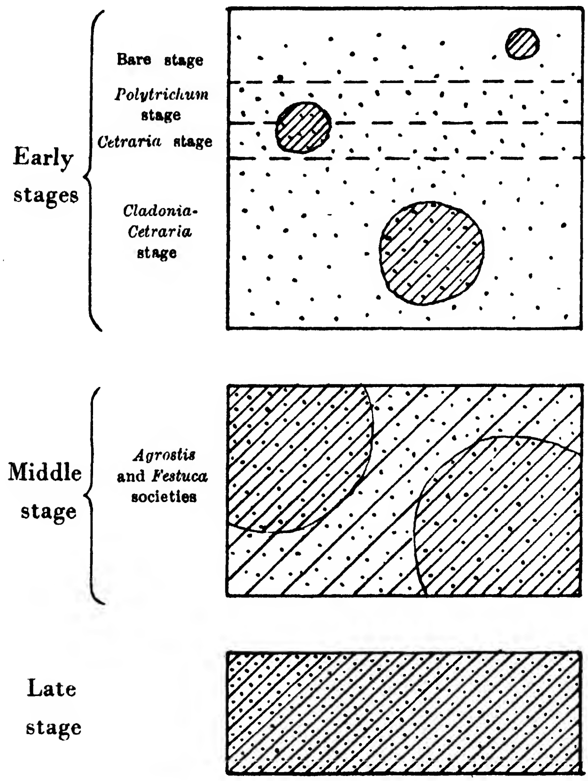


Fig. 2. Diagram of the three major stages in the succession from bare soil to the adult *Festuco-Agrostidetum*. The dots represent individuals of *Festuca ovina* and the diagonal lines *Agrostis* spp. Only progressive or the peak states of the vegetation in the three stages are represented.

plants play the leading part. Outwards from the bare soil at the foot of the eroding sand bank there is a series of communities dominated respectively by *Polytrichum piliferum*, *Cetraria aculeata* and *Cladonia silvatica* with *Cetraria*. The chief higher plants present are *Festuca ovina* and species of *Agrostis* (*A. alba* and *A. tenuis* are found, but since no difference in their behaviour was noted they are considered together). *Festuca ovina* is scattered over all three communities, *Agrostis* is rare and in small patches only.

From these nuclei *Agrostis* eventually spreads through the whole area and a pattern is discernible, distinct at first, less obvious later. Abundant *Agrostis*, with some *Festuca*, is accompanied by dominant *Cladonia silvatica* forming large grey circular patches: these are set in a background of grey-purple consisting of mixed *Cetraria* and *Cladonia* studded with numerous plants of *Festuca* and relatively few shoots of *Agrostis*. This is the second or Middle stage. The third stage is a more intimate mixture of *Agrostis* and numerous but small *Festuca* plants set in a carpet of dominant *Cladonia*.

Fig. 2 depicts the peak events in the succession showing the change in dominance among the lower plants, *Polytrichum* giving way to *Cetraria* and *Cetraria* to *Cladonia* as well as the gradual spread of the higher plants *Festuca* and *Agrostis* and the changing relations between them. A summary of important data is given in Table II.

Table II. *Summary of important data in the chief communities of the Early, Middle and Late stages of the succession*

		Early stages					Middle stages		
		Bare stage	*Poly-trichum* stage	*Cetraria* stage	*Cladonia-Cetraria* stage with *Festuca*	*Cladonia* stage with *Agrostis*	*Festuca* society	*Agrostis* society	Late stage
Polytrichum piliferum	No. per 6·25 sq. cm.	<1	44	22	1	0	<1	<1	<1
Cetraria aculeata	Frequency %	0	28	100	99	49	56	38	6·5
	Cover %	0	<1	65	30	4	11	4·5	<1
Cladonia silvatica	Frequency %	<1	6	66	100	100	100	100	100
	Cover %	<1	<1	8	56	92	81	91	80·5*
Festuca ovina	No. per sq. m.	15	33	21	19	6·6	52	27	86
	Cover %	1·2	8·1	7·7	6·3	1·8	6·9	2·5	2·6
	Av. area per plant in sq. cm.	11·0	24·5	36	33	26·5	13·6	9·0	3·0
Agrostis spp.	No. of shoots per 0·05 sq. m.	145	92	59	115	50	25	64	135
Loss on ignition	0–1·3 cm. surface soil	0·55	0·49	0·72	0·90	1·05	1·55	1·46	2·90

* This value is low compared with the others because of the larger area occupied by higher plants.

If the lower forms only were concerned the succession would stop at the *Cladonia-Cetraria* stage; it is only the presence of the higher plants which enables the *Cladonia* eventually to overcome *Cetraria* producing a continuous grey carpet. But the effects produced by *Festuca* and *Agrostis* proceed at different rates: the social *Agrostis* accelerates the lichen succession much faster than the isolated tufts of fescue with their strictly local influence.

The aggregates of *Agrostis* and *Festuca* may be likened to two streams fed from a common watershed. At first they flow in independent but converging channels (first stage): later (second stage) they join and share a common channel, but the waters mingle slowly and it is only when the mixture is

intimate and homogeneous that the last stage is reached. The comparison may be extended to include the lower plants which may be likened to the suspended load of particles of different sizes present in the waters near the sources of the stream. The fractional separation of the particles as the separate and combined streams flow on represents the gradual and successive elimination of the dominants *Polytrichum* and *Cetraria* of the first two zones; only the finest particles representing *Cladonia* remain to the end. And if the separate streams have different carrying powers, the *Festuca* branch greater than the *Agrostis*, then the rate of deposition will vary accordingly. In the *Agrostis* branch the heavier particles will be quickly dropped, in the *Festuca* branch more slowly and some of the coarser will be carried into and even some distance along the common channel.

The communities represented and already mentioned are, however, only the crests of a series of waves, for in the troughs between succeeding crests are series of retrogressive and progressive phases. It is as if the needs of the plants periodically outran the means of subsistence, degeneration follows and

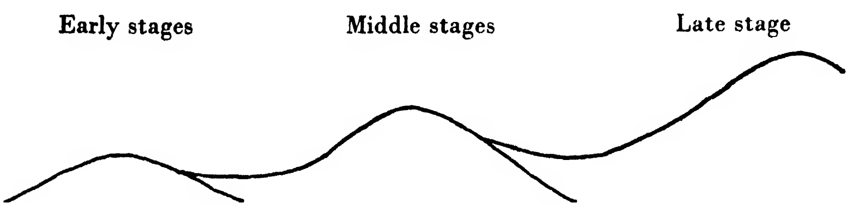


FIG. 3. The diagram represents the wave-like succession towards the *Festuco-Agrostidetum*. The vegetation after development to a certain stage degenerates in whole or in part and a new progressive series is initiated. Partly degenerate communities develop to the next peak. The development of the vegetation on soil eroded to the erosion pavement has not been worked out.

a fresh start is made. Moreover, each successive wave is bigger and probably lasts longer. The simple diagram (Fig. 3) is intended to illustrate this, the crests of the waves representing the peak of development in each stage, the descending parts of the curve retrogression and the ascending progression. The change in humus content is significant (Table II).

Two examples of the phenomenon are outlined here: details are given in the sequel.

During the building up and dominance of the *Polytrichum* stage, sand, blown from the adjoining eroding surface, gradually accumulates forming a layer several centimetres thick over the erosion pavement. On this soil the lichen communities succeed the *Polytrichum*. But in the change from the *Polytrichum* stage to the *Cetraria* stage and from the *Cetraria* to the *Cladonia-Cetraria* stage *Polytrichum* is gradually covered by the lichens and dies. Now *Polytrichum* provides the anchorage for the lichens and when it decays the lichen cover disintegrates and exposes the sand. Erosion follows and varying

amounts of sand are blown away. In the extreme case all the accumulated sand is removed, exposing once again the erosion pavement. With stabilization of the soil a fresh start is made in rebuilding by *Polytrichum*, and a *Polytrichum* stage is followed by one with *Cetraria* dominant which, differing in some respects from the earlier one is called the persisting *Cetraria* stage because it may last for many years. The presence of *Festuca* does not appreciably affect this cycle and while the details are different where *Agrostis* occurs the course of events is much the same, the *Agrostis* dying, the accompanying lichen carpet of *Cladonia* disintegrating and exposing the soil to erosion. Further progress in building on the foundations of the persisting *Cetraria* stage is dependent on a fresh acquisition of blown sand or an invasion by *Agrostis*. Fig. 4 is a diagrammatic representation of this cycle.

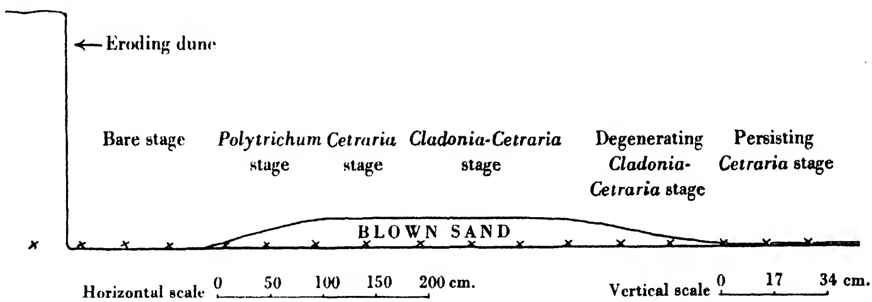


FIG. 4. Next the sand bank the sand is blown away exposing a flint strewn surface (crosses represent flints). *Polytrichum* invasion results in the accumulation of blown sand over this erosion pavement. On the sand fixed by *Polytrichum* a lichen cover develops until the anchoring *Polytrichum* is killed out. Thereafter the lichen cover disintegrates and the exposed soil is or may be eroded down once again to the erosion pavement.

The other example shows that retrogression also follows the crest of development in the Middle stages. Starting with communities which in many respects closely resemble the Late or Adult stage, but which are distinguished from it mainly by the uneven distribution of *Festuca* and *Agrostis*, the partial or complete mortality among the higher plants is followed by a partial or complete disruption of the lichen cover and by exposure of the soil. Here again erosion may proceed to different degrees: in the extreme case to the erosion pavement. But erosion may be arrested at different stages and a whole series of communities is found from bare soil or the erosion pavement through communities on partially eroded sand with *Polytrichum*, *Cetraria* and *Cladonia* the most important plants. These communities closely resemble the members of the initial progressive series but unlike them they do not constitute a true developmental succession: they represent a slipping back down the inclined plane of retrogression to different places, whence from the wreck of the pre-existing vegetation new starts are made and development reaches different stages. The data for the "loss on ignition" show the dissipation of the hardly won store of humus (Table IX, p. 23).

In the adult stage the stock of humus has risen to 2·90 % and the vegetation appears much more stable. But even this is not permanent for in 1936 there are obvious signs of retrogression. No data, however, are presented.

The discussion of these phenomena follows the detailed description of the plant communities.

Methods of vegetation analysis

The primary recognition of the different communities is based partly on the presence or absence of species but mainly on the relative areas covered by each. To obtain objective data, not only to distinguish the communities which are our immediate concern but similar communities in the succession on podsolized soils, I have used a statistical method. For the moss and lichen communities and synusiae I use a wooden rectangular frame, 10 × 50 cm. (= 0·05 sq. m.), i.e. one-twentieth of a square metre, with wire strung across at 2·5 cm. intervals giving 80 squares each of 6·25 sq. cm. The number of squares in which each species occurs gives some idea of its scatter in the sample, but none of the area occupied. This is estimated and recorded as cover per cent. For each community data of this kind are obtained from 14 (sometimes 10, and occasionally 7 when the material is not abundant) samples each of 0·05 sq. m. For *Polytrichum* the number of shoots for one small square (always the same square in the frame) is recorded in each sample. From these data we obtain the constancy (percentage occurrence in 14 samples), the dispersion or frequency (percentage occurrence in the total number (14 × 80) of small squares), the cover per cent and for *Polytrichum* the average number of shoots per unit of 6·25 sq. cm. as well.

The constancy figures are of little or no value in differentiating communities where all the chief species are present in a sample plot of the size chosen. Hence the values are not given. The frequency is a much more sensitive criterion and its values taken together with cover per cent form an adequate descriptive and differentiating basis.

For some of the higher plants, *Festuca ovina* in particular, larger units were used, varying in size according to the area covered by the community. These units were always in the form of strips, sometimes discontinuous, 30 cm. wide, and varying in total length from about 5 to 20 m. In these were recorded the total number of established plants, and for *F. ovina* the area covered by each plant. Data for *Agrostis* were obtained by counting the number of shoots in 7–14 plots each of 500 sq. cm.—in a few communities in plots ¼ × 4 m.—and this unit was always used in counting seedlings of *Teesdalia nudicaulis* and *Festuca*. All the results are expressed in units of 1 sq. m. or 0·05 (one-twentieth) sq. m.

DETAILED DESCRIPTION OF THE COMMUNITIES

(1) *The Early stages*

The Bare stage (Tables III and IV). The first successful colonizer of a young blow-out is *Polytrichum piliferum* which ultimately dominates in a belt down the middle. Flanking it and between it and the eroding dune faces are marginal strips of bare soil which continue as bare strips so long as the dune faces retreat. Meanwhile the vegetation in the trough develops.

In the area there is one young blow-out whose trough is still being eroded and several older active blow-outs with, in the aggregate, a long marginal strip of bare sand. The marginal strip as well as the young blow-out has a flint-strewn surface, unstable and hostile to plant establishment. In the young blow-out 98% of the ground is bare: in the strip the figure is smaller (89%) because of the marginal outposts of colonizing *Polytrichum*. The soil is coarse

Table III. *Data of some habitat factors in the "moss-lichen succession with fescue" of the Early stages: particle size by sieving, depth of the "gravel layer", humus content and* pH

		Bare stage: Young blow-out	Bare stage: Marginal in older blow-outs	*Poly-trichum* stage	*Cetraria* stage	*Cladonia-Cetraria* stage	Persisting *Cetraria* stage: Derived from degenerate *Cladonia-Cetraria* stage	Persisting *Cetraria* stage: In young blow-out
Particle size by sieving in per cent	>3 mm.	7·75	5·90	0·29	0·27	0·95	11·96	13·51
	2–3 mm.	2·42	1·00	0·29	0·18	0·20	1·54	1·38
	1–2 mm.	10·36	4·26	1·25	0·90	1·02	3·64	4·72
	0·5–1 mm.	9·80	8·86	4·79	3·17	4·06	5·72	7·74
	<0·5 mm.	69·67	79·98	93·38	95·48	93·77	77·14	72·65
Depth of "gravel layer" in cm.		0	0 to variable	6·8	6·6	6·3	0	0
Humus in fraction passing 0·5 mm. sieve		0·52	0·58	0·49	0·72	0·90	1·45	0·88
*p*H of fraction passing 0·5 mm. sieve		4·9	5·2	5·5	4·7	4·6	4·7	4·7

textured (less than 80% of the sand passes the 0·5 mm. sieve and 7% or more is "gravel" with diameters over 2 mm.); it is deficient in humus (0·52–0·58%) and for this area has a relatively high *p*H (4·9–5·2). The width of the strip varies from place to place (1·2–2·3 m.) and from year to year, depending on the weather as it affects the relative rates of dune retreat and *Polytrichum* advance. During the four years 1931–5 the dune retreated 61 cm. at one place, while the *Polytrichum* belt advanced only 45 cm.; thus, during this period the bare zone widened by 16 cm. If we assume an average retreat of the dune of 15 cm. per annum then in a bare zone 2·3 m. wide the strip next the advancing *Polytrichum* will have been exposed for approximately 15 years. In the part of the bare zone next the dune faces conditions of course vary; at one time it is covered by fallen sand, at another, when this has been blown away, the erosion pavement is exposed up to the foot of the cliff.

Table IV. *Statistical data for the vegetation of the "moss-lichen succession with fescue" of the Early stages*

		Bare stage						Persisting *Cetraria* stage	
		Young blow-out	Marginal in older blow-outs	*Polytrichum* stage	*Cetraria* stage	*Cladonia-Cetraria* stage	De-generating *Cladonia-Cetraria* stage	Derived from degenerate *Cladonia-Cetraria* stage	In young blow-out
		Data for lower plants between fescue tussocks							
Bare soil	Cover %	98	89	0	0	1	2 (35)	12	17
Polytrichum piliferum	Frequency %	1	<1	100	97	32	32	97	98
	Cover %	<1	7	100	48	<1	3	19	76
	No. per 6·25 sq. cm.	<1	<1	44	22	1	<1	2	14
Cetraria aculeata	Frequency %	0	0	28	100	99	90	100	96
	Cover %	0	0	<1	65	30	60	63	22
Cladonia silvatica	Frequency %	<1	0	6	66	100	86	71	52
	Cover %	<1	0	<1	8	56	22	14	<2
C. furcata	Frequency %	1	0	1	19	72	49	33	8
	Cover %	<1	0	<1	2	13	13	9	<1
Other lichens	Cover %	0	0	0	1	0	0	3	<1
Cladonia uncialis	Frequency %	0	0	<1	12	16	5	10	5
C. crispata	Frequency %	0	0	<1	3	<1	0	2	7
C. coccifera	Frequency %	0	0	0	10	6	2	15	2
C. verticillata	Frequency %	0	0	0	0	<1	<1	1	<1
C. pityrea	Frequency %	0	0	0	1	<1	<1	0	<1
C. bacillaris, C. fimbriata, C. floerkiana	Frequency %	0	0	0	5	2	<1	3	1
Alectoria chalybeiformis	Frequency %	0	0	<1	7	<1	0	5	11
Diploschistes scruposus	Frequency %	0	0	0	0	0	0	2	0
Height of lichens in cm.		0	0	<1	1	1·7	1·3	1	1
		Data for higher plants							
Festuca ovina	No. of established plants per 1 sq. m.	20	10	33	21	19	20	13	4
	Cover %	1	1·3	8·1	7·7	6·3	7·1	3·7	0·5
	Av. size of individual in sq. cm.	8·7	13·2	24·5	36	33	35	28	11·4
Teesdalia nudicaulis	No. per 1 sq. m. June	21	5	0	0	6	4	0	3
Aira praecox	No. per 1 sq. m.	0	3	0	0	1·5	0	0	6
Rumex acetosella	No. per 1 sq. m.	1	0	0	0	2·5	3	1	0

I am indebted to Mr J. Ramsbottom and to Dr W. Watson for naming the lichens.

The pioneers in the bare stage are mainly higher plants whose difficulties in establishment and spread are clear from their scarcity over an area whose different parts have been exposed for different periods of time. *Festuca* with 10–20 plants per sq. m. is the commonest, the individual plants averaging 9–13 sq. cm.; collectively they cover about 1% of the total area. *Agrostis* is absent from the young blow-out but in the 20×0·3 m. sample strip there are only five colonies covering 1·5% of the area. By December 1935 all these colonies had died. *Teesdalia* is found mostly in the more stable part of the

strip next the *Polytrichum* belt. In the young blow-out the numbers vary from year to year (as also doubtless in the strip) from 1·5 per sq. m. in July 1933 to 21 in 1934. *Aira praecox*, even less numerous than *Teesdalia*, occurs chiefly on the uneroded fallen sand at the foot of the sand bank.

Among the lower plants *Polytrichum* is the most important, occurring as isolated shoots, small colonies, or as well-established outposts next the *Polytrichum* belt, together covering about 7% of the strip and less than 1% in the blow-out. Bits of lichens (*Cetraria aculeata*, *Cladonia silvatica* and *C. furcata*) lie loose on the surface but fail to become established except with the aid of *Polytrichum* or of the higher plants, *Festuca* and *Agrostis* (*v.* pp. 17–18).

As to the origin of these pioneers, *Teesdalia* and *Aira* arrive of course by seed, but many *Teesdalia* at any rate die before reaching maturity: in April 1934 there were 47 per sq. m., in July 21. In the strip *Festuca* seedlings are found, 0·1 live and 0·1 dead per sq. m.; it is thus doubtful if successful establishment follows except possibly in suitably wet years. The bulk if not all the fescue and certainly all the bent is derived from surviving parts brought down with sods from the eroding dune. *Polytrichum* comes from the same source; bits of the plant are blown about by the wind, a few are buried and give rise to new shoots. Every isolated shoot examined showed this origin. There is no evidence of establishment from spores.

It is possible that in the widening of a young blow-out the flinty soil may remain exposed, be colonized by *Polytrichum* and the vegetation develop to a later stage without any accumulation of sand. Such a later stage has been examined, but as its essential features are those of the persisting *Cetraria* stage its description is deferred (p. 16).

The Polytrichum *stage* (Tables III and IV). The outposts of *Polytrichum* in the Bare stage increase in size and eventually coalesce to form a green belt of almost pure *Polytrichum* fringing the bare strip at the foot of the eroding dune. Sand blown from this bare strip is caught by the *Polytrichum* shoots which may be buried, but new shoots push their way through, produce a mat of rhizoids which, binding the sand, make it firm under foot. Sods of *Polytrichum*—bound sand, dug up and broken vertically, reveal, under suitable conditions of soil moisture, superimposed strata each about 0·5 cm. thick. Hence the *Polytrichum* belt usually grows on blown sand overlying the erosion pavement, in this area at an average depth of 6·8 cm. (Fig. 4).

The surface soil thus has all the properties of a sifted sand (93% passes the 0·5 mm. sieve and only 0·6% is "gravel"). The humus content is very low, 0·49%, and the *p*H relatively high, 5·5. The humus and *p*H are interrelated and the decreases from the Bare stage are bound up with changes during erosion. The width of the belt varies, being determined by the area covered by recently blown sand. Thus during storms sand may be blown across the *Polytrichum* on to the *Cetraria* stage, causing a return to *Polytrichum* dominance. As commonly met with the belt is from 2 to 3 ft. (60–90 cm.) wide.

P. piliferum is dominant throughout with an average of 44 shoots per unit of 6·25 sq. cm. Here and there *Polytrichum* dies in small round patches, 6–20 cm. across; these become denuded but are eventually recolonized. They do not show any gradual enlargement, and Prof. Brooks, to whom I am indebted for the test, reports that no fungus is present. The cause, or at any rate one of the causes, is birds' droppings, but exactly how it operates has not yet been investigated. The shoots of *Polytrichum* provide excellent anchorage for bits of lichen blown on to the belt: the clinging *Cetraria aculeata* shows the highest frequency (28%), next comes *Cladonia silvatica* with 6%, whilst *C. furcata*, *C. uncialis*, *C. crispata*, *Alectoria chalybeiformis* show 1% or less. The cover per cent of the lichens is negligible. The lichen population must, however, vary from time to time, even at the same spot and over short periods. A fresh coat of sand buries and kills most of the lichens; wet weather, especially driving rain, causes *Cetraria* to loosen its grip and be removed—a phenomenon which explains the persistence of the *Polytrichum* stage in hollows where water accumulates during heavy rain. Thus development to the *Cetraria* stage is checked both by dry and by wet windy weather.

Competition in the *Polytrichum* belt discriminates among the higher plants. *Teesdalia* germinates and seedlings are established but none attains maturity; for example in December 1932 there were 34 seedlings per sq. m. but no adults in July 1933. No *Aira praecox* was found. The perennials *Festuca* and *Agrostis*, on the other hand, not only hold their own but increase their number and area, as well as causing a reduction in the numbers of *Polytrichum* per unit area. Of fescue plants there are now 33 per sq. m. with an average size of 24·5 sq. cm., covering 8·1% of the total area. Establishment by seed is difficult: in December 1932 there were 64 seedling fescues per sq. m. and in July 1933, after a dry spring, 6 live and 24 dead were counted. It seems likely that the number of fescue plants is increased in the *Polytrichum* belt, but that the numbers will vary according as the weather favours or is hostile to their establishment. Thus, since in the *Cetraria* and *Cladonia-Cetraria* stages no further additions by seedlings take place, the numbers of fescues in these stages will vary from place to place in the later stages of the succession. There is no evidence that *Agrostis* can establish itself by seed, but the plants incorporated from the Bare stage spread.

The Cetraria *stage* (Tables III and IV). In the absence of further additions of blown sand (erosion pavement at 6·6 cm.) *Cetraria* grows more quickly than any other lichen and forms a narrow belt about 60 cm. wide. As explained already its width fluctuates and in December 1935 the belt in many places was practically obliterated. The soil is essentially the same as in the *Polytrichum* stage, with 95% passing the 0·5 mm. sieve and the small fraction of 0·5% classed as "gravel". The humus content has increased to 0·72% and the acidity to *p*H 4·7, presumably due to the influence of *Polytrichum*.

Cetraria aculeata has a frequency of 100, but does not yet form a complete

cover (65 %) over the *Polytrichum*. Without the stimulus of further additions of sand *Polytrichum* itself fails to maintain its numbers—there are now only 22 per 6·25 sq. cm.—and the cover per cent is 48, although its frequency is still high (97 %). On this stage bits of *Cladonia silvatica* continue to arrive, become established and grow, but while the frequency has jumped to 66 % the cover per cent is still 8 only. *C. furcata* has a much slower rate of increase with a frequency of 19 and a cover per cent of 2. At the same time other lichens show an increase or appear for the first time: *C. uncialis* has a frequency of 12 %, *C. crispata* 2·5 %, *Alectoria chalybeiformis* 7 %, *C. cocciferia* 10 %, *C. pityrea* 1 %, *C. fimbriata*, *C. floerkiana* and *C. bacillaris* taken together 5 %. Collectively these cover a small area, about 1 %. The common height of *Polytrichum* and *Cetraria* is about 1 cm.

The fescues have increased in average size to 36 sq. cm., together covering 7·7 % of the total area, but their numbers are fewer (21 per sq. m.) which, as explained already, does not necessarily mean the death of any, and, of course, fusion may occur. Increase by seed is apparently difficult; in December 1932 there were 15 seedlings per sq. m., in July 1933, 9 dead and less than 1 per sq. m. alive. Among the *Teesdalia* seedlings there was 100 % mortality: 11 per sq. m. in December and none in the following June. No *Aira praecox* was noted.

The Cladonia-Cetraria *stage* (Tables III and IV). In the shelter of the *Cetraria* and *Polytrichum* there is a rapid increase in the amount and growth of *Cladonia silvatica*. The two lichens grow up together thoroughly well mixed and become codominant in a habitat which physically is the same as those of the *Polytrichum* and *Cetraria* stages with the erosion pavement at an average depth of 6·3 cm. But there is a further slight increase in humus (0·90 %) and in acidity (*p*H 4·6).

It is clear that the limits of the *Cetraria* belt on the side away from the *Polytrichum* belt is determined by the relative rates of growth and spread of *Cetraria* and *Cladonia*. Here, on blown sand, *Cladonia* grows faster and partly suppresses the *Cetraria* within a period of 2 or 3 years.

For the dominants comparison of the data for frequency and for cover shows that *Cladonia silvatica* has increased (frequency from 66 to 100 and cover per cent from 8 to 56), whilst *Cetraria*, maintaining its maximum frequency, has lost in cover from 65 to 30 %. *Cladonia* has in fact increased its area partly at the expense of *Cetraria*, whose remains are detected below the lichen mat. The surviving *Cetraria* are "drawn up" like an oak in a beech-wood. Meanwhile *C. furcata* shows a striking increase in frequency from 19 to 72, but a low increase in cover per cent from 2 to 13. The only other lichen to show an increased frequency is *C. uncialis* (from 12 to 16), the others which survive show a decrease, *Alectoria*, *Cladonia crispata*, *C. coccifera*, *C. pityrea*, and taken together *C. fimbriata*, *C. bacillaris* and *C. floerkiana*. *C. verticillata* is recorded for the first time in the succession but has a frequency of less than 1.

The *Cladonia* and *Cetraria* form a continuous mat of an average thickness of 1·7 cm. which kills out the *Polytrichum* leaving an average of one live shoot per 6·25 sq. cm. It seems at first puzzling why *Polytrichum* should be unable to grow through the lichen mat as it is able to grow through sand; additions of sand do in fact stimulate branching (Leach, 1931), but with no further addition the number of live shoots per unit area falls. New shoots do grow up from the soil into the lichen cover but they die, the moss, with its inefficient conducting system, being apparently unable during dry weather to supply the necessary moisture from the soil. This conclusion is supported by the results of an experiment (Table V) where the *Polytrichum* rhizoids were provided with

Table V. *The effect on* Polytrichum *growth of the maintenance of dry and moist air round the shoots, under covers of different kinds*

No.	Cover	Wax seal	Air round shoots	Remarks on growth
1	No cover	–	Moist	Old shoots continued growth and new shoots arose from the soil. Later, leaves remained appressed and tips became brown
2	No cover	+	Dry	Growth started from old plants and new shoots arose from the soil. Growth in both quickly checked
3	Dry sand	+	Dry	No growth
4	Wet sand	+	Moist	New growth from old plants; no new shoots from the soil
5	*Cetraria*	–	Moist	New growth from old plants and new shoots from the soil. Shoot tips withered where they projected beyond *Cetraria*
6	*Cetraria*	+	Moist	New growth from old plants and new shoots from the soil
7	Cotton-wool	–	Moist	Ditto
8	Cotton-wool	+	Moist	Ditto

moisture but the parts above ground were subjected to dry or moist conditions. The natural *Polytrichum* sod was transferred to glass tubes 2·5 cm. in diameter so that the soil surface was about 2 cm. below the upper edge of the tube. In some tubes the soil surface was sealed with wax, the *Polytrichum* shoots projecting above it; in others it was left unsealed. The *Polytrichum* was covered with different kinds of material, namely, sand, *Cetraria* and cotton-wool. All tubes were watered from below and this was the only source of supply for those without wax seals. Those with wax seals were watered from above as well, except in two sets, one with no cover and one with dry sand. All the tubes were covered on the outside with black paper.

In all tests the soil was moist, but only where the air above was also moist (whether due to evaporation from the unsealed wet soil below or by the addition of water from above) did the *Polytrichum* continue growth, either from the apex, by new shoots from the side or from the underground parts penetrating the wax seal. In the two tests where the air was dry (Nos. 2 and 3) there was no growth, or growth started but was quickly checked. All the new growth showed etiolation, and where the air round the shoots was less moist, as in No. 1, the new leaves remained appressed and their tips later became brown as also did the leaves of shoots which projected beyond the cover of

Cetraria into the dry air of the laboratory. Thus it seems clear that the maintenance of a supply of moisture round the young shoots is necessary for their survival. The field phenomena may thus be explained: new shoots which grow from the soil into the lichen mat during a favourable wet period, dry up in a drought. There is no evidence that *Cetraria* has a toxic effect on *Polytrichum*. Thus during development from the *Polytrichum* to the *Cladonia-Cetraria* stage the lichen cover over *Polytrichum* becomes thicker and denser, *Polytrichum* fails to surmount this kind of burial and dies. The dead stems persist for some time affording a fast anchorage, but in time they decay and break off.

In this mat of mixed lichen *Festuca* plants are scattered, showing 19 per sq. m. of an average size of 33 sq. cm., the whole covering 6·3% of the area. The individual plant is slightly smaller than in the *Cetraria* stage partly because of partial death and partly because these rabbit grazed tufts are closely set about by the lichens and their limits are much better defined; in the *Polytrichum* and *Cetraria* stages they are more spreading with "ragged" edges. Establishment by seed probably does not occur: in July 1933 there was one live seedling per sq. m. and 9 were dead, whilst in the previous December there were 19 alive. The removal of competition with *Polytrichum* may account for the persistence of *Teesdalia*: per sq. m. there were 1·5 in December 1932 and 6 in June 1933. *Aira* and *Rumex* are represented by 1·5 and 2·5 respectively per sq. m.

The disintegrating Cladonia-Cetraria *stage* (Table IV). The fescue is not numerous enough to replace *Polytrichum* as an effective anchorage for the lichen mat. Disintegration takes place and bare soil is eventually exposed, the area uncovered varying from time to time as the mat is dispersed over the bare soil or blown away. The final result is denudation followed by erosion, which may proceed until the erosion pavement is once again exposed. As the soil varies much no data are given.

The differential action of the dispersing forces and the new conditions are evident in the changed relations of the chief species. The frequencies of *Cetraria* and *Cladonia* spp. are reduced by varying amounts but wider variation is found in the data for cover per cent: *Cetraria* increases from 35 to 60%, *Cladonia furcata* remains the same, while *C. silvatica* decreases considerably. The area of denuded soil varies: in 1933, 35% was bare, in 1934 only 2%, while in 1935 large areas had their lichen cover completely removed. With its lichen competitors destroyed *Polytrichum* spreads: in 1934, 3% of the area was occupied, in 1935 a much larger but undetermined part.

There are 20 fescue plants per 1 sq. m. of an average size of 35 sq. cm. and covering 7·1% of the area. In April 1933 there were 7 live and 5·4 dead seedlings per 1 sq. m., but no data were obtained for survival later in the year. The chances were against any surviving in the dry year 1933. In April 1933 there were 3·8 *Teesdalia* per sq. m. and 3 *Rumex acetosella*.

The persisting Cetraria *stage* (Tables III and IV). With time—the process has been observed during the last few years—erosion may uncover the erosion pavement. *Polytrichum* spreads and development proceeds to a *Cetraria* stage which persists for many years until further development is made possible either by the addition of blown sand or by the spread of *Agrostis*. The surface is flinty, the "gravel" fraction is 12% and the fraction passing the 0·5 mm. sieve falls to 77%. The humus content is 1·45% and the *p*H 4·7. Bare soil and flints occupy 12% of the area. From the cover of lichens on large flints Dr W. Watson estimates their age as from 12 to 15 years.

The contrast between the behaviour of *Cladonia silvatica* in the persisting *Cetraria* stage and in the *Cetraria* stage is striking. In the former the *Cladonia* exists as small pieces and many are quite loose or unattached; it is clear that the conditions are hostile to the spread of this lichen. In spite of the longer time available for growth and spread the values for frequency and cover per cent are only slightly higher than in the *Cetraria* stage (71 and 14 compared with 66 and 8). The data for *Cetraria* are the same, and for *Cladonia furcata* slightly higher, and also proportionately higher than for *C. silvatica*. *Polytrichum* shows the same frequency but a much reduced cover per cent and number of shoots per unit area. All the other lichens in the area are present here except *Cladonia pityrea* and they have much the same values as in the *Cetraria* stage. But the *Cetraria* stage has no *Cladonia verticillata* nor *Diploschistes scruposus*. The last named grows on well-decayed remains of fescue tussocks.

The difficulties of establishment for *Festuca* are shown by the data for the seedlings; in December 1932 there were 9 live seedlings per sq. m., in June 1933, 0·7 live and 3 dead. Thus it is likely that no (or at most few) additions have been made to the fescue survivors from the earlier stages. Adults show a reduction in number, size and area covered. The smaller number of fescue is due, in part at least, to the death of some; 1 dead tussock per sq. m. was recorded, but in addition there are dead, much decayed remains covered by *Diploschistes*. The reduction in size is due to the splitting up of larger tufts which die away in the centre. If it is correct to assume that these fescue tussocks have survived from the Bare or *Polytrichum* stage, then they must be from 20 to 40 years old. There are no adult *Teesdalia*; in December 1932 there were 4 seedlings per sq. m., in the following June there were no adults. There is no *Aira*, and *Rumex acetosella* is represented by 1 plant per sq. m.

Mention has already been made of the possibility of the erosion pavement remaining exposed during the earlier stages of widening of the blow-out. Stabilization by *Polytrichum* is followed by the development of a community of essentially the same kind as the persisting *Cetraria* stage. The soil is similar, 14·9% is "gravel" and 73% passes the 0·5 mm. sieve. The humus content is less, 0·85%, and the *p*H is 4·7. Bare soil and flints occupy 17% of the area.

The conditions are slightly more severe than in the persisting *Cetraria* stage, and this is reflected in the failure of *Cladonia silvatica* and *C. furcata*

to spread. *C. silvatica* has a frequency of 52% but a cover per cent of 2 only. Even *Cetraria*, although it has a high frequency, has the relatively low cover per cent of 22, while *Polytrichum* has a high frequency, a high cover per cent and 14 shoots to 6·25 sq. cm. Among other lichens *Cladonia crispata* and *Alectoria* have higher values for frequency than in any other stage.

There are only 4 fescues to the sq. m. each 11·4 sq. cm. in area, and together covering 0·5% of the area. On the other hand there are 2·7 *Teesdalia* and 6·1 *Aira* per sq. m.

Thus in the moss-lichen cycle a stage is reached comparable in many respects with the community developed directly on the erosion pavement of the trough of the blow-out.

The effect of Festuca ovina *on the moss-lichen succession.*

In the different stages of the moss-lichen cycle the effect of fescue was studied by examining the dispersion of the lichens on and immediately around the fescue tussock. The data (Table VI) show that the moss-lichen succession

Table VI. *Frequency data of lichens and* Polytrichum piliferum *on and in the immediate neighbourhood of* Festuca *tussocks in the moss-lichen succession of the Early stages. The corresponding data for the moss-lichen succession between the tussocks are given in brackets*

	Bare stage	*Polytrichum* stage	*Cetraria* stage	*Cladonia-Cetraria* stage
Polytrichum piliferum	7 (<1)	93 (100)	71 (97)	7 (32)
Cetraria aculeata	38 (0)	80 (28)	87 (100)	51 (99)
Cladonia silvatica	13 (0)	35 (6)	76 (66)	90 (100)
C. furcata	2 (0)	5 (1)	28 (19)	58 (72)
C. uncialis	<1 (0)	<1 (<1)	10 (12)	8 (16)
C. crispata	0 (0)	0 (<1)	5 (2·5)	<1 (<1)
C. coccifera	0 (0)	0 (0)	<1 (10)	0 (6)
C. fimbriata, C. bacillaris, C. floerkiana	0 (0)	0 (0)	2 (5)	<1 (2)
Alectoria chalybeiformis	<1 (0)	0 (<1)	0 (7)	0 (<1)

is expedited and carried a stage further. The fescue tussocks act as nuclei for the establishment of *Polytrichum* and the lichens; there is no *Polytrichum* stage but already in the Bare stage there is a definite approach to the proportions of *Cetraria* and *Cladonia silvatica* found in the *Polytrichum* stage; in the *Polytrichum* stage there is a maximum of *Polytrichum* (93%), but the approach to the *Cetraria* stage is much closer in the high figure for *Cetraria* (80%), with an intermediate figure for *Cladonia silvatica* (35%); in the *Cetraria* stage a decrease in *Polytrichum* (71) is accompanied by a slight further increase to a maximum in *Cetraria* (87), and a marked increase in *Cladonia* (76) and in *C. furcata* (28); finally in the *Cladonia-Cetraria* stage, *Polytrichum* almost disappears (7), *Cetraria* decreases markedly (51), and *Cladonia silvatica* and *C. furcata* reach their maxima with 90 and 58% respectively. It is clear that essentially the same sequence of change is taking place as in the moss-lichen

succession itself, but that the stages are somewhat telescoped and the process is accelerated.

The failure to obtain the maximum possible values for the dominants in the respective stages is due to the method employed by which the practically lichen-free surface of the grazed tuft of fescue is taken together with the immediate surround. If the surround alone had been considered the figures for the lichens would have been higher, and in fact in the *Cladonia-Cetraria* stage the succession in the surround is carried a stage further to the almost complete dominance of *Cladonia silvatica* (suggested in the data by the reduced frequency of *Cetraria*) which forms a kind of ruff round the fescue tussock. A point of significance which is demonstrated better in the effect of *Agrostis* on the succession is that where *Cladonia silvatica* starts on more even terms with *Cetraria* it is able to suppress it more completely than in the moss-lichen succession where the growth and spread of *Cladonia* is handicapped by exposure. That fescue provides this shelter is clear from examples in other parts of Lakenheath Warren where isolated tufts have an incomplete ruff of *Cladonia* best developed on the sheltered north-east side. The influence of fescue is, however, quite local and the numbers of this plant are too few appreciably to affect the cycle in the moss-lichen succession.

The Early stages of the succession with Agrostis.

As we have already seen the establishment of *Agrostis* in the Bare stage is a rare event conditioned by the weather, and it is the difficulties attending its ecesis which make possible the cycle of vegetational change just described. There is no good evidence to show that *Agrostis* is established from seed; on the contrary everything points to its origin in the large sods which fall from the eroding cliff and carry living plants with them. The network of live and dead roots and stolons prevents the complete erosion of the sand so that the succession starts on low mounds of fine sand overlying the erosion pavement (Watt, 1937, Fig. 6, p. 103) which is thereby protected from further erosion and is at a slightly higher level than the erosion pavement in the surrounding Bare stage. These low mounds are commonly circular and pass, so to speak, back into and through the *Polytrichum*, *Cetraria* and *Cladonia-Cetraria* stages already described. In the meantime their own vegetation develops and from these nuclei *Agrostis* spreads into and alters the surrounding vegetation. Two series of phenomena therefore call for comment, first the change in the vegetation on the low mounds and secondly the changes induced by the spread of *Agrostis* into the different stages of the moss-lichen cycle.[1]

The change in the vegetation on the low mounds. Complete data are lacking. Data for frequency were supplemented in December 1935 by data for cover

[1] It is not possible in all examples to separate the original patch from the surrounding area to which *Agrostis* has spread. Hence some of the records may be from transitional stages.

per cent, and at this time also soil samples were taken. By then all the *Agrostis* patches in the Bare stage had died.

The erosion pavement lies at 7–10 cm. from the soil surface under blown sand the analysis of which (Table VII) shows the high percentage of sand

Table VII. *Data of some habitat factors in the* Agrostis *patches in the Early stages; particle size by sieving, depth of the "gravel layer", humus content and* pH

		Bare stage	*Polytrichum* stage	*Cetraria* stage	*Cladonia-Cetraria* stage	*Cladonia* stage	Degenerate *Cladonia-Cetraria* and *Cladonia* with *Agrostis*		*Agrostis* patch in persisting *Cetraria* stage, marginal and central
Particle size by sieving in per cent	>3 mm.	No data	0·20	0·52	0·41	0·26	0·23	0·52	6·51
	2–3 mm.	,,	0·20	0·52	0·31	0·43	0·39	0·21	1·60
	1–2 mm.	,,	0·61	0·72	1·14	1·28	0·78	1·03	4·47
	0·5–1 mm.	,,	3·40	3·82	5·26	4·01	3·73	7·22	9·57
	<0·5 mm.	,,	95·59	94·42	92·88	94·02	94·86	91·02	77·85
Depth of "gravel layer" in cm.		,,	9·0	8·2	10·4	7·1	8·1	8·0	0–0·5 (6·0)
Humus in fraction of soil passing 0·5 mm. sieve		,,	0·45	0·73	0·84	1·05	0·82	1·10	1·26
*p*H of fraction passing 0·5 mm. sieve		,,	4·4*	4·3*	4·1*	4·4	4·1*	4·4	4·4

* These values were obtained from samples collected in December 1935.

(93–96 %) passing the 0·5 mm. sieve and the low values for gravel (0·4–1·0 %). With development the humus content increases but the *p*H varies little. The humus content of the surface soil of the sod in the *Polytrichum* stage is low because the original surface of the sod is covered by recently blown sand.

The general effect of *Agrostis* on the succession (Table VIII) is essentially the same as that of the individual fescue plants, differing mainly in degree; the rate of development is hastened so that (for example in the *Cetraria* zone) the patch with *Agrostis* is in the *Cladonia-Cetraria* stage. But there are two important differences between the succession with *Agrostis* and the moss-lichen succession. The presence of *Agrostis* and the fine sand of the surface soil of the mounds in the Bare zone are favourable to the anchorage and growth of *Cladonia silvatica* so that *Cetraria* starts only slightly ahead with a frequency of 34 compared with 27 for *Cladonia*. With development the *Cetraria* maintains its lead in the frequency values up to the *Cetraria* zone where the *Cladonia* comes level with it. By this stage however the cover per cents which were the same in the *Polytrichum* zone now show *Cladonia* ahead with 30 and *Cetraria* with 24 % only. Later, in the *Cladonia-Cetraria* zone, the frequency of *Cetraria* drops from 95 to 70, whilst that for *Cladonia* rises to the maximum possible (100). The same kind of change is shown in the figures for cover per cent; that for *Cetraria* decreases whilst the figure for *Cladonia* is doubled. These data show that where conditions are favourable to *Cladonia* and the two lichens start together, *Cetraria* is suppressed to a greater degree than in the moss-lichen succession, where *Cetraria* starts well ahead of *Cladonia*. Secondly, the

Table VIII. *Statistical data for* 1933–4 *of the vegetation of the* Agrostis *patches in the Early stages. (The corresponding data for the "moss-lichen succession" are given in brackets.) Note: the data printed in italics were obtained in December* 1935 *and are comparable only with each other because of the considerable changes following the drought*

		Bare stage	*Polytrichum* stage	*Cetraria* stage	*Cladonia-Cetraria* stage	*Cladonia* stage	Two stages in rebuilding after retrogression of the *Cladonia* stage and the *Cladonia-Cetraria* stage		*Agrostis* patch in persisting *Cetraria* stage: Marginal	Central
					Lower plants					
Polytrichum piliferum	Frequency %	20 (<1)	84 (100)	74 (97)	20 (32)	<1	4	22	15 (97)	20
	Cover %	(7·3)	*31* (100)	*27* (48)	*1·5* (<1)	0	*<1*	*<1*	3 (19)	5
	No. of shoots per 6·25 sq. cm.	(<1)	*10* (44)	*9* (22)	*<1* (1)	0	0	0	<1 (2)	<1
Cetraria aculeata	Frequency %	34 (0)	89 (28)	95 (100)	70 (99)	49	95	90	100 (100)	74
	Cover %	(0)	*5* (<1)	*24* (65)	*18* (30)	4	*32*	*30*	57 (63)	17
Cladonia silvatica	Frequency %	27 (0)	67 (6)	94 (66)	100 (100)	100	98	100	99 (71)	100
	Cover %	(0)	*6* (<1)	*30* (8)	*61* (56)	92	*48*	*64*	30 (14)	72
C. furcata	Frequency %	5 (0)	19 (1)	25 (19)	38 (72)	42	63	61	54 (33)	59
	Cover %	(0)	*<1* (<1)	*6* (2)	*11* (13)	4	*8*	*5*	5 (9)	6
C. uncialis	Frequency %	1 (0)	3 (0·3)	15 (12)	9 (16)	2	6	12	15 (10)	10
C. crispata	Frequency %	0 (0)	<1 (<1)	1 (2·5)	0 (<1)	0	0	0	0 (2)	0
C. coccifera, C. pyxidata	Frequency %	0 (0)	<1 (0)	4 (10)	<1 (6)	<1	3	5	11 (15)	4
C. pityrea	Frequency %	0 (0)	0 (0)	0 (1)	0 (<1)	<1	<1	<1	<1 (0)	<1
C. bacillaris, C. fimbriata, C. floerkiana	Frequency %	0 (0)	<1 (0)	1 (5)	0 (2)	<1	<1	<1	2 (3)	<1
C. verticillata	Frequency %	0 (0)	0 (0)	0 (0)	0 (<1)	0	2	1	3 (1)	<1
Bare	Cover %	(89)	*40* (0)	*1·5* (0)	*<1* (1)	0	*12*	*2*	8 (12)	4
Height of lichen cover in cm.		—	*1*	*1·5* (1)	*2·5* (1·7)	3·4	*2·75*	*2·9*	1·4 (1)	2·1
					Higher plants					
Agrostis spp.	No. of shoots per 0·05 sq. m.	145	92	59	115	50	38	91	74	49
Festuca ovina	No. of plants per 1 sq. m.	0	0	—	14·2	6·6	8·6		8·6*	8·6*
	Cover %	0	0	4	3·1	1·8	2·5		0·5*	0·7*
	Av. size per plant in sq. cm.	0	0	—	21·3	26·5	29·2		6·3*	8·3*
Teesdalia nudicaulis	No. per 1 sq. m.	92	86	0	0	0	0	1·5	0	0
Aira praecox	No. per 1 sq. m.	29	0	0	0	0	3	3	0	0
Rumex acetosella	No. per 1 sq. m.	0	0	0	3	4·3	0	3	0	3

* These figures are based on data from 0·35 sq. m. only.

presence of *Agrostis* provides anchorage for *Cladonia* even when the *Polytrichum* is exterminated, so that further development is still made possible, in fact development to a community in which *Cladonia* covers 92 % of the area and *Cetraria* only 4 %. In this series *Cladonia furcata* plays a minor part; the frequency values show a steady but slow rise to a maximum of 42 while the cover per cent has a maximum of 11 only in the *Cladonia-Cetraria* zone.

Not only does the presence of *Agrostis* give *Cladonia silvatica* a flying start, it also enables it to grow taller, to a height in fact twice that of the lichen cover in the *Cladonia-Cetraria* stage (3·4 cm. against 1·7 cm.). This would appear to account for the further suppression of *Cetraria* and of *Cladonia furcata*.

This community with *Cladonia silvatica* clearly the dominant lichen is not stable. The *Agrostis* dies or the numbers of its shoots are much reduced (*v.* next paragraph) and the lichen cover disrupts into "scabs" exposing bare soil between. At the same time there is a readjustment of the different lichens to the new conditions: *Cladonia silvatica* decreases and *Cetraria* increases. In fact the values for frequency and for cover of the chief species are similar to those found in the *Cladonia-Cetraria* stage. 12 % of the soil is bare, but the presence of some live *Agrostis* and the network of dead stolons puts a check on complete denudation.

Throughout the series the numbers of *Agrostis* shoots change. In the Bare stage the number of shoots per 0·05 sq. m. is high (145), due mainly to the influence of fresh layers of blown sand stimulating shoot production; thereafter there is a fall, then a rise to 115 followed by another fall to 50 in the community with *Cladonia silvatica* dominant (where in fact one plot had as few as 5 shoots) and a further fall to 38 in the disrupted stage following. In the last two stages the dead remains of *Agrostis* are abundant under the lichen mat.

The full story of what happens to the fescue is not clear from the data. In the first place there were no fescues in the *Agrostis* patches in the Bare and *Polytrichum* stages, and incomplete data were obtained from the *Cetraria* stage. But there is every reason to suppose that the fescue plants found in the later stages of the succession came with the *Agrostis* sod and did not arise subsequently from seed. With regard to the later stages it will be noted that the numbers per sq. m. are very much less than in the zones of the moss-lichen succession with fescue. The percentage cover is less and so is the average size of the individual plant. Within the series there is a reduction in number, little difference in cover per cent, but the average size of the plant increases from the stage in the *Cladonia-Cetraria* zone to the next stage with dominant *Cladonia silvatica*. What actually happens is that some of the original fescue plants die (their remains are seen below the lichen mat), some increase in size slowly, while others die away in the centre and surviving parts are on the way to becoming separate small plants. These groups were mostly recorded as single plants; if each part had been counted as a separate plant the numbers

per unit area would have been much larger and the average size per plant less. The final result is a change in the size of the individual fescue plant and a much smaller cover per cent than in the moss-lichen succession with fescue.

The annuals *Aira praecox* and *Teesdalia* behave as one might expect. In the open early stages their numbers are high; they are absent from the later closed stages and *Aira* reappears in the disintegrating community where conditions also appear suitable for *Teesdalia* although none was recorded.

The effect produced on the stages of the moss-lichen succession with fescue by the invasion of Agrostis. From the low mounds as a base *Agrostis* spreads radially into the adjoining stages of the moss-lichen-fescue succession. Complete records of its influence were not made, but one set of data illustrates the kind and degree of change brought about.

A circular patch of *Agrostis* in the persisting *Cetraria* stage showed a core with much *Cladonia silvatica* and a peripheral zone with much less. In the centre there is a small patch of blown sand, about 6 cm. deep, which is presumed to be the relic of a mound carrying *Agrostis* and from which surviving *Agrostis* has spread outwards. The soil of the patch as a whole is similar to that of the persisting *Cetraria* stage, but the total soil passing the 1 mm. sieve is about 5% higher. The humus content is slightly less and the *p*H 4·4 against 4·7. A small amount of blown sand added after erosion to the flint layer took place would explain these differences.

The two zones, outer and inner, represent two stages, Early and Late in the development of the community derived from the persisting *Cetraria* stage by the invasion of *Agrostis*. Compared with the persisting *Cetraria* stage the outer zone shows much less *Polytrichum*, a slightly lower cover per cent of *Cetraria* and a much increased cover per cent for *Cladonia silvatica*. *C. furcata* shows an increased frequency but a lower cover per cent, whilst *C. coccifera* shows a slightly lower value, although it is still higher than that for any other community. At the same time the area of bare soil is reduced from 12 to 8% and the height of the lichen cover increases from 1 to 1·4 cm. These distinct trends become more marked in the late, central core. *Polytrichum* shows little change although the figures are the opposite of what one would expect. *Cetraria* has now lost its high status and the dominance of *Cladonia silvatica* is clearly asserted; *Cetraria* has a cover of 17% only (reduced from 57), while the value for *Cladonia* has gone up from 30 to 72%. The area of soil left bare is now halved and the height of the lichen cover has increased to 2·1 cm.

As to the higher plants the number of *Agrostis* shoots has gone up from 0 in the persisting *Cetraria* stage to 74 in the outer zone, then down to 49 in the inner. Fescue in the outer zone has 8·6 plants per sq. m. (13 in the persisting *Cetraria* stage), the number remaining the same in the inner zone. The cover per cent is now very much smaller, reduced in fact from 3·7 to 0·5 and 0·7, whilst the average size is also very much less. In the central core, however, the survivors are larger than those of the outer zone—a record which agrees

in essentials with the changes taking place in the main line of succession on the mounds carrying *Agrostis* and for which the explanation already given holds. Dead fescues are revealed by the removal of the lichen cover.

The same sort of change is produced by *Agrostis* invading stages in the moss-lichen-fescue succession. The invasion of the partially disintegrated *Cladonia-Cetraria* stage and the rebuilding of the degenerate *Cladonia* stage with *Agrostis* lead to a rapid increase in the *Cladonia*. *Agrostis* shoots increase to 91. The effect on fescue is the same as before: the number per sq. m. is reduced from 19 to 8·6, cover per cent from 6·3 to 2·5 and the size of the individuals from 33 to 29·2 sq. cm.

It is clear that under these conditions the communities are unstable, but despite vicissitudes revealed in the cycle of progression and degeneration the humus content of the soil increases and the vegetation as a whole progresses towards a higher level of development. The changes noted foreshadow what in fact does happen: *Agrostis* pervades the whole area, but patches of abundant *Agrostis* with few fescues and much *Cladonia* are discernible in a general background of *Agrostis* with many fescues and *Cladonia* less in evidence.

(2) *The Middle stages* (Tables IX and X)

Suitable material for the study of the immature *Festuco-Agrostidetum* is found on the side of the Barton Mills–Brandon road opposite to the dune complex where the Early stages were studied. The whole area is invaded by *Carex arenaria* but neither its numbers nor its habit appears to exert a dominating influence; in fact the conditions which determine the cyclic behaviour of *Festuca* and *Agrostis* affect *Carex* in the same way.

The two facies with varying proportions of *Festuca* and *Agrostis* are called for convenience the *Festuca* society and the *Agrostis* society. They grow on blown sand overlying the erosion pavement (at 6·5 and 9·7 cm. respectively).

Table IX. *Data of some habitat factors in the Middle stages and in the Adult stage: particle size by sieving, depth of the "gravel layer", humus content and* pH

		Middle stages							
		Agrostis society	*Festuca* society	Degenerate *Agrostis* society on partially eroded soil	Degenerate *Festuca* society on soil eroded to the gravel layer	*Cetraria* stage on slightly eroded soil	*Poly-trichum* stage	Bare stage	Adult stage
Particle size by sieving in per cent	>3 mm.	0·61	0·25	0·49	13·12	0·40	8·98	12·19	1·07
	2–3 mm.	0·58	0·47	0·41	1·14	0·30	1·76	1·76	0·64
	1–2 mm.	2·68	2·34	1·90	4·29	1·50	4·68	4·48	3·63
	0·5–1 mm.	8·39	5·72	5·36	4·80	5·52	6·61	6·10	10·47
	<0·5 mm.	87·74	91·22	91·84	76·65	92·28	77·97	75·47	84·19
Depth of gravel layer in cm.		6·5	9·7	7·7	0	8·1	0	0	2·4
Humus in fraction passing the 0·5 mm. sieve		1·46	1·55	1·45	1·03	0·84	0·74	0·50	2·90
pH of fraction passing the 0·5 mm. sieve		4·4	4·5	4·6	4·7	4·3	4·9	5·0	4·4

Table X. *Statistical data of the vegetation in the Middle stages and in the Adult stage*

		Middle stages							
		Agrostis society	*Festuca* society	Degenerate *Agrostis* society	Degenerate *Festuca* society	*Cetraria* stage	*Polytrichum* stage	Bare stage	Adult stage*
Lower plants									
Polytrichum piliferum	Frequency %	5	2	8	58	67	87	9	5·5
	Cover %	<1	<1	2·7	29	26	66	1	<1
	No. of shoots per 6·25 sq. cm.	<1	<1	<1	1·8	2	16	1	0·6
Cetraria aculeata	Frequency %	38	56	78	73	83	45	1	6·5
	Cover %	4·5	11	29	16	30	2	0	<1
Cladonia silvatica	Frequency %	100	100	95	52	44	4	<1	100
	Cover %	91	81	40	10	8	0	0	80·5†
C. furcata	Frequency %	15	19	19	1	3	<1	0	34
	Cover %	<1	1	<1	<1	0	0	0	1·5
C. uncialis	Frequency %	24	12	22	7	2	<1	<1	16·5
C. coccifera	Frequency %	<1	<1	1	<1	<1	<1	0	<1
C. pityrea	Frequency %	0	0	0	0	<1	0	0	<1
C. verticillata	Frequency %	0	<1	0	0	0	<1	0	0
C. bacillaris, C. fimbriata, C. floerkiana	Frequency %	<1	<1	1	0	0	<1	0	<1
Bare soil	Cover %	1	1	28	38	41	33	97	0
Height of lichen cover in cm.		2·5	2·8	1·1	1·0	1·1	0·8	0	2·5
Higher plants									
Agrostis spp.	No. of shoots per 0·05 sq. m.	64	25	26	12	11	3	0	135
Festuca ovina	No. per 1 sq. m.	27	52	10	123	30	49	49	86
	Cover %	2·5	6·9	<1	11·7	3	2·7	2·4	2·6
	Av. size of plant in sq. cm.	9·0	13·6	6·2	9·1	10·3	6·7	4·7	3·0
Teesdalia seedlings per 1 sq. m. (April 1934)		4·3	11·4	40	6	222	30	39	1·5
Aira praecox per 1 sq. m.		0	0	0	0	0	0	0	70
Rumex acetosella shoots per sq. m.		2·9	4·3	0	2	1	0	0	17
Lugula campestris shoots per 1 sq. m.		0	0	0	0	0	0	0	223
Carex arenaria shoots per 1 sq. m.		81	106	272	31	18	0	0	119

* Besides the species recorded in the table there occur *Polytrichum juniperinum* with a frequency of 17% and *Cladonia alcicornis*, *Lophozia excisa* and *Ptilidium ciliare* with a frequency less than 1%.

† An apparently low value, only because of the high numbers of higher plants.

Thus in both (Table IX) the bulk of the sand passes the 0·5 mm. sieve and the percentage of "gravel" is small. The *p*H values are the same in both (4·5 and 4·4), the humus content is also the same (1·46 and 1·55) and higher than in any of the earlier stages. Thus the habitats are the same and we now know that the differences in the communities can only be explained by reference to their history.

In the *Festuca* society the number of *Agrostis* shoots per 0·05 sq. m. is only 25, in the *Agrostis* society 64 (Table X). On the other hand fescues are more numerous, cover a larger area and the individual plants are larger than in the *Agrostis* society (52, 6·9 and 13·6 compared with 27, 2·5 and 9·0

respectively). *Carex arenaria* has respectively 106 and 81 shoots per sq. m. *Rumex* occurs in much smaller numbers, while for no obvious reason there are more *Teesdalia* in the *Festuca* than in the *Agrostis* society (11·4 and 4·3 per sq. m.).

The tendencies noted in the Early stages towards a splitting up of the fescue tussocks are clearly shown here. The data for fescue in the *Festuca* society compared with those for the stages in the moss-lichen-fescue succession show a large increase in number of plants, a small drop only in the percentage area covered and a marked fall in the size of the individual plants; while the data for fescue in the *Agrostis* society compared with those for the *Agrostis* patches (on blown sand) in the Early stages again show a large increase in the number of plants but a small increase in the area covered and a big drop in the size of the individual plants. Thus fescue is apparently adjusted to the changing conditions by decreasing the size of the individual plant and increasing its numbers.

The infiltration of *Agrostis* into the fescue branch of the succession brings about a change in the lichen cover so that it now closely resembles that in the *Agrostis*: *Cladonia silvatica* becomes dominant and *Cetraria* quite subsidiary. Slight differences still separate them: for example, there is a 10% difference in the cover of *Cladonia silvatica* (91% in the *Agrostis* and 81% in the *Festuca*) which now has a frequency of 100 in both, and correlated with that *Cetraria* is less important in the *Agrostis* than in the *Festuca* society (frequency 38 and 56, cover per cent 4·5 and 11 respectively). The other lichens as well as *Polytrichum* are unimportant. The thickness of the lichen mat is about the same in both (2·5 and 2·8 cm.).

Neither of these societies is stable: the *Agrostis*, *Carex* and some of the *Festuca* die, the lichen mat disrupts and the soil is exposed to erosion. Thus between the intact societies and the bare soil of the re-exposed erosion pavement there is a series of stages in which five representative communities have been examined. These are the degenerate *Agrostis*, degenerate *Festuca*, *Cetraria*, *Polytrichum* and Bare stages (data: Tables IX and X).

These five communities cannot be regarded as a continuous regressive sequence: they are really communities in some of which residual elements from the original societies exist side by side with progressive complexes derived from them or from outside sources, temporary or relatively permanent halts during which efforts are made by plants able to put up with the conditions to rebuild the vegetation anew. But their similarity to some of the stages in the early moss-lichen-fescue succession is obvious, reflecting the repetition of similar sets of conditions. A detailed analysis of the data is therefore not called for: important points only need be stressed.

The derivation of some of these degenerate stages from the two societies is obvious. Thus using the data for fescue as a criterion, the degenerate *Agrostis* stage (only slightly degenerate and on scarcely eroded soil) shows a

small number (10) of fescue plants covering a small area (0·7 %), while the degenerate *Festuca* stage (much degenerate and on soil eroded down to the erosion pavement) the number of fescue is high (123) and the cover per cent (11·7) higher even than in the intact *Festuca* society. This is due to recolonization and spread from the relict fescue tussocks which form sand ballasted hillocks. Similarly in the degenerate *Cetraria* community, parts are clearly derived from the *Agrostis* and parts from the *Festuca* society: in the former there are 17 as against 42 plants in the latter, and the cover per cent varies in the same direction—1·7 against 4·4. In the *Polytrichum* and Bare stages disruption and erosion have gone so far that a composite origin cannot be made out, but owing to establishment from seed the numbers of fescue are relatively high. Each plant is small and collectively they cover a relatively small area.

While much of the fescue survives the disintegration of the community in which it occurs and is able to establish itself from seed even on the inhospitable, though stable, erosion pavement, *Agrostis* suffers almost complete annihilation and appears unable to invade by seed. Its numbers dwindle and the odd plants are probably survivors from the original community: it is quite absent from the Bare stage. *Carex arenaria* suffers a similar fate with, however, an apparent increase in the degenerate *Agrostis* stage. That *Carex* has been present in the *Polytrichum* stage at least, if not also in the Bare stage, is clear from the presence in the soil of the dead deep-going roots. In the degenerate *Festuca* stage most of the *Carex* appears to be composed of recent invaders.

Although the behaviour of *Carex* forms part of a separate study, data on the depth of origin of the living shoots show that where the soil is denuded the rhizome lies at a greater depth than where the lichen cover is intact: and further that in the intact *Agrostis* and *Festuca* societies dead rhizomes are found at greater depths than the living shoot-bearing rhizomes.

	Degenerate *Cetraria* stage	Degenerate *Festuca* society	Degenerate *Agrostis* society	*Agrostis* society	Adult *Festuco-Agrostidetum*
Depth of origin of *Carex arenaria* shoots in cm.	8·5	7·7	3·3	2·3	2·9

The conclusion is reached that as the community develops the shoot-bearing rhizomes come nearer the soil surface and that the development of a continuous lichen cover bears some causal relation to it.

With soil denudation, as one would expect, the numbers of *Teesdalia* increase to 30–40 per sq. m.: 6, in the degenerate *Festuca* stage is an exception and the high number of 222 in the *Cetraria* stage was obtained in December 1935 and is therefore not strictly comparable. The other data were obtained in April 1934.

The lichens in the degenerate stages behave as they do in the similar stages

of the early part of the succession. On the disruption of the lichen mat *Cladonia silvatica* loses its pre-eminence, finally becoming negligible in the *Polytrichum* and Bare stages; *Cetraria*, on the contrary, becomes more abundant, attaining pre-eminence in the *Cetraria* stage, and thereafter declining in importance. Other lichens play a quite insignificant part.

Polytrichum, almost exterminated in the *Festuca* and *Agrostis* societies, creeps slowly back to significance, ultimately becoming the most abundant plant in the *Polytrichum* stage with values for frequency, cover per cent and number per unit area comparable with those in the rather extreme form of the persisting *Cetraria* stage. In the Bare stage it is a pioneer with low values.

In 1934 the beginnings of degeneration were already obvious in some examples of the *Agrostis* and *Festuca* societies, and since then one patch of the degenerate *Agrostis* society has been denuded and the surface sand removed to a depth of 2·5 cm. No doubt the rate has been hastened by the drought partly because of the check to recolonization by *Polytrichum* and *Festuca*. Favourable wet years will enable the soil stabilizers to spread and erosion may be checked before the erosion pavement is reached. But while the weather conditions affect the relative rates of degeneration and progression the cycle of change is independent of them and is determined by the vegetation itself.

(3) *The Adult* Festuco-Agrostidetum (Tables IX and X)

Within this area of brown forest soil there is a community which is regarded as the mature fescue-bent community. The erosion pavement is overlaid by a thin layer of blown sand 2·4 cm. deep; 84 % of the surface sand passes the 0·5 mm. sieve, 10·5 % has a particle size between 0·5 and 1 mm. diameter and 1·07 % is "gravel". The *p*H is 4·4. Thus so far as acidity and particle size are concerned the soil is similar to that in the immature communities. But there is an important difference in the humus content which now stands at the relatively high level of 2·9 %, the highest value in the sere and twice that in any previous stage.

The community is closed, consisting of an intimate mixture of *Agrostis* and large numbers of small fescue set in an almost pure carpet of *Cladonia silvatica*. *Agrostis* shoots per 0·05 sq. m. reach the high number of 135: *Festuca* now has 86 plants per sq. m. of an average size of 3·0 sq. cm. together covering only 2·6 % of the area. Thus the process of the breaking up of the fescue and its diffusion through the community is probably now complete and a state of equilibrium reached.

A second important change is the large increase in the number of individuals of *Aria praecox* (found in 10 out of 14 plots), a sporadic plant in all seral stages except the first Bare stage where it occurs on sand fallen from the cliff and not yet blown away. There are 70 plants to the sq. m., but the lack of space to branch out (and perhaps the poor soil conditions) is shown by the small

number of shoots per plant; there are only 79 shoots to 70 plants, little more than 1 shoot per plant. The same is true in lesser degree of *Rumex acetosella* (in half the plots) which has 17 shoots per sq. m. The number of *Teesdalia* plants betrays inability to grow in a closed community (only one plant was found in the 14 plots), in this respect a marked contrast to *Aira*.

The appearance of *Luzula campestris* for the first time in the sere marks a third important difference. Present in 11 out of 14 plots, it has an average of 11 shoots per 0·05 sq. m.

Carex arenaria occurs in nearly all the plots (13) but shows no sign of becoming dominant: per 1 sq. m. there are 119 shoots whose leaves have an average length of 8·4 cm. As already noted the rhizomes bearing live shoots lie near the surface at an average depth of 2·9 cm.

In the lichen synusia *Cladonia silvatica*, with an average height of 2·5 cm., is clearly dominant over all other species but has a cover per cent of 80 only because of the ground covered by the large numbers of shoots of higher plants. Other lichens cover a negligible proportion of the area; even their frequencies are low, *C. furcata* with 34, *C. uncialis* with 16·5 are the next highest to *C. silvatica* with 100. *Cetraria* has the low value of 6·5; the others have values less than 1. Although these other lichens contribute little to the vegetation cover the presence of a relatively large number of species is interesting. Among them *Cladonia alcicornis* appears for the first time in the sere.

Similarly among bryophytes *Polytrichum juniperinum*, *Lophozia excisa* and *Ptilidium ciliare* make their first appearance in the mature community. The two liverworts occur in one plot only. *Polytrichum juniperinum* is found in 11 out of 14 plots and has a frequency of 17: *P. piliferum* on the other hand is more local, occurring in half the number of plots with the much lower frequency of 5·5. The Polytricha together cover 1·5% of the area and average 0·6 shoots per 6·25 sq. cm.

While in 1934 there was no actual disruption in this community there is evidence that degeneration takes place. For example, in one plot there were only 38 live shoots of *Agrostis*, but there was much dead *Agrostis* and *Luzula*; at the same time the number of individuals of *Aira praecox* was higher than in any other plot. This conclusion is confirmed by observation in 1936 when *Agrostis* shoots were obviously fewer although no counts were made.

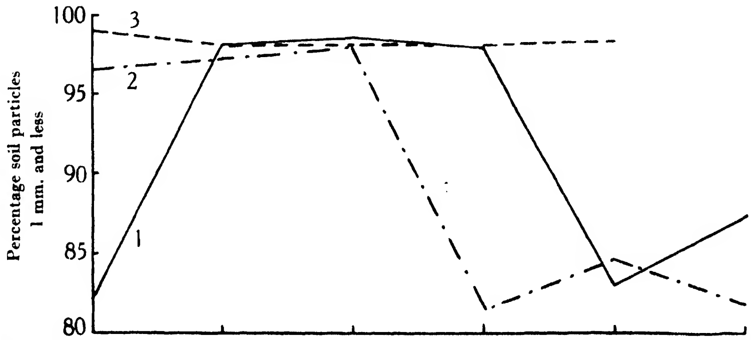
Discussion of results

(1) *The habitat*

Sieving analysis. The present, with the recent past, is not the first time that erosion has taken place in this area, for the existing banks consist of wind-blown sand overlying a truncated profile capped by an erosion pavement. The erosion pavement therefore separates soil in place with flints scattered through it from the overlying wind-sifted flint-free sand. The physical and

chemical properties of these two differ and the fact must be kept in mind in interpreting the data of physical analyses, humus content and acidity.

Within the blow-outs themselves the reaction of the soil to vegetational change results in the two processes of sand accumulation and sand dispersal separated in space and in time by a relatively stable soil, all three phases forming part of a cycle or wave of change. The whole forms a patchwork with a pattern changing in time and within any one short period consisting of patches of relatively stable soil and vegetation set in a shifting background of progression and retrogression, of accumulating and dispersing sand. The physical constitution of the surface soils therefore varies and the three graphs (Fig. 5) show the variation in the fraction passing the 1 mm. sieve.



(1) Early Moss-lichen succession	Bare stage	*Polytrichum* stage	*Cetraria* stage	*Cladonia-Cetraria* stage	Persisting *Cetraria* stage	Persisting *Cetraria* stage with *Agrostis*
(2) Middle stages	*Agrostis* and *Festuca* societies	Degenerate *Agrostis* society	*Cetraria* stage	Degenerate *Festuca* society	*Polytrichum* stage	Bare stage
(3) Early stages with *Agrostis*	In *Polytrichum* stage	In *Cetraria* stage	In *Cladonia-Cetraria* stage	*Cladonia* stage	Degenerate *Cladonia-Cetraria*	

FIG. 5. The percentage of soil particles 1 mm. and less in the surface 1·3 cm. of soil is graphed to show the erosion cycle (1) and a retrogressive series (2). (3) shows that the *Agrostis* communities begin and continue (until retrogression leads to erosion) on wind-blown sand.

(1) shows the complete cycle of change from the flinty soil of the Bare stage with its high percentage of larger particles through the wind-sifted sands, almost wholly of fine sand, bearing the *Polytrichum*, *Cetraria* and *Cladonia-Cetraria* stages back again to the flinty soil of the persisting *Cetraria* stage. Added to the end of this graph is the corresponding value for the *Agrostis* patch in the persisting *Cetraria* stage showing the initiation of fine sand accumulation, the beginning of another wave. (2) shows the retrogressive part of the cycle in the Middle stages where disruption of the *Agrostis* and *Festuca* societies on wind-blown sand allows erosion to proceed, it may be even to the erosion pavement. (3), for the *Agrostis* patches in the moss-lichen succession of the Early stages, shows consistently high values for fine sand and further that the *Agrostis* patch starts in the Bare stage on fine sand and continues

on it, the erosion in the retrogressive phases having taken place but slightly or not at all at the time the samples were taken.

Humus content. From crest to crest of the successive waves of vegetational change the humus shows a graduated increase from 0·55% in the Bare stage to 0·90% in the *Cladonia-Cetraria*, 1·50% in the *Agrostis* and *Festuca* societies and 2·90% in the adult stage. But humus content reflects stages of instability as well. In the moss-lichen succession of the Early stages there is a progressive increase, with a slight set-back in the *Polytrichum* stage, due to fresh sand accumulation, to the *Cladonia-Cetraria* stage. No data were obtained for the retrogressive phases in this cycle, but from those of the Middle stages a descending series of values is obtained, 1·50, 1·45, 0·84, 1·03, 0·74 and 0·50%. These values correspond with the distribution of humus in a vertical section of the surface soil of the *Agrostis* and *Festuca* societies.

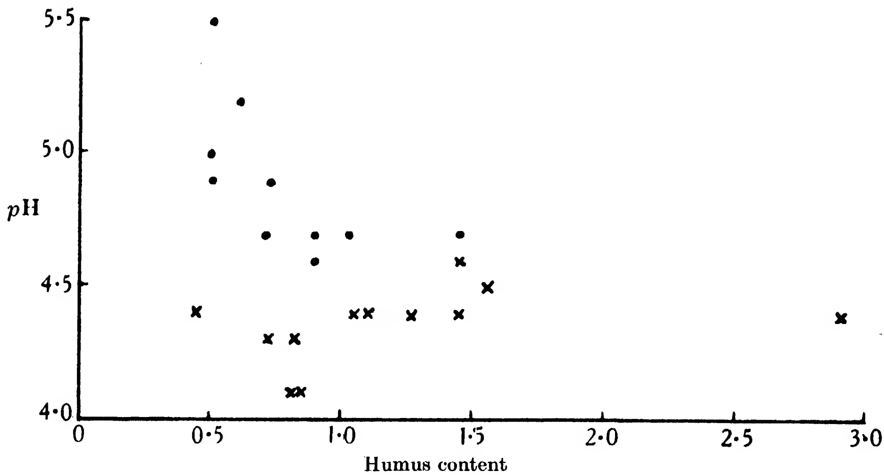


FIG. 6. The plotted points show the relation between pH and the humus content: the dots represent the relation in communities without *Agrostis*, the crosses in communities with *Agrostis*.

The humus content of a stable soil may be a function of time. Thus the persisting *Cetraria* stage, stable for 20 years or so, has the relatively high value of 1·45%. And it is tempting to argue that the higher values for the crest of the wave in the Middle stages and for the Adult stage imply stability for a longer time. They may well mean this but there is no certainty, for a cycle of change may be short circuited by incomplete retrogression and erosion and the humus content represent an addition to an already fairly large store. From the point of view of the succession as a whole the important fact remains that there is an accumulation of humus.

The hydrogen-ion concentration. Two main factors affect the pH values: first, the origin of the soil, whether from above or below the erosion pavement;

secondly, the amount of humus present. The *p*H of the soil immediately below the erosion pavement is relatively high, approximately 5·0, while that of the blown sand is about 4·4. The change from high values to low (due to humus accumulation) and from low to high (due to uncovering the original soil) may be seen in the moss-lichen succession with values in the successive stages of 5·1, 5·5, 4·7 and 4·6, and in the retrogression in the Middle stages with values generally increasing from 4·4 to 5·0. On the other hand in all communities with *Agrostis* the *p*H remains at a fairly constant level irrespective of the humus content.

The relationships between the *p*H and humus content are seen in Fig. 6 where the plotted points suggest two curves: one (the dots) representing the decrease in *p*H of the soil with increase in humus and the other (the crosses—values from all communities with *Agrostis*) a stable acidity round about *p*H 4·4 but with a varying humus content. The figure, *p*H 4·4, apparently represents an "end" acidity phase under the existing vegetation.

(2) *The flora*

The poverty of the flora is undoubtedly due to the infertility of the soil, only *Festuca ovina* and the two species of *Agrostis* being at all well represented among perennial plants. Among annuals only *Teesdalia nudicaulis* and *Aira praecox* are found: *Alchemilla arvensis*, *Cerastium semidecandrum*, *Myosotis collina*, *Veronica arvensis*—to mention only a few of the less exacting widely distributed annuals in Breckland—are absent. Other studies to be published later confirm the view that the poorest soils in Breckland exclude all annuals except *Teesdalia* and *Aira*.

The same species of higher plants occur throughout the sere. To this general statement *Luzula campestris* is an important exception, for it is confined to the mature community where its occurrence may be bound up with the set of conditions produced by a relatively high humus content. And the suggestion may be extended to explain the limitation to the same stage of the lower plants *Polytrichum juniperinum*, *Lophozia excisa*, and *Ptilidium ciliare* and even to the gradual infiltration of several species of lichen after the Early *Polytrichum* stage.

(3) *Competition and the succession*

Polytrichum piliferum is essentially a pioneer colonizing the open spaces by vegetative reproduction from bits surviving in sods fallen from the eroding bank. Its ability to face an inhospitable inorganic world is further shown by its admirable adaptation not only to survive but to flourish under repeated additions of thin layers of blown sand. But in competition with other plants it fails miserably: as soon as the soil becomes stable *Cetraria* and *Cladonia* gradually form a light-excluding cover fatal to it. Its short stature is a weakness; and if in the later stages of the succession odd individuals grow

taller and survive, *Polytrichum* remains an insignificant component—yet important because when the lichen cover disrupts these individuals get their chance and grow out into unoccupied soil.

Its competitive power is also small because of low "root" efficiency, for, where there is an adequate light intensity as in low diffuse plants of *Festuca ovina* and in open *Agrostis* patches of the *Polytrichum* stage the numbers of *Polytrichum* are much less than in the adjoining fescue-bent-free areas. Only *Teesdalia* (and perhaps *Aira*) appears as an exception, for no seedlings survive to maturity in the *Polytrichum* stage.

The two lichens *Cetraria aculeata* and *Cladonia silvatica* with somewhat similar growth form are yet differentiated in dominance partly by growth form and partly by habitat. Both are reproduced from wind-blown fragments and neither is able to "strike root" in the Bare stage, but while, under suitable conditions, *Cladonia* grows faster and taller, it is the more clinging, more xerophytic *Cetraria* which first becomes dominant over *Polytrichum*. Here the time-relation is important, for with a good start *Cetraria* may for a time at least hold its own with the taller growing *Cladonia*. On the other hand where the two start even, under habitat conditions favourable to *Cladonia* as well as to *Cetraria*, *Cladonia* becomes dominant. This is seen in the lichen cover of *Agrostis* patches. Habitat also decides the relationship between these two: the more xerophytic *Cetraria* is able to maintain its dominance where stony conditions prevail as in the persisting *Cetraria* stage. On the other hand the provision of shelter by *Agrostis* shoots by *Festuca* tussocks, in shallow cart-tracks and on the north-east side of low mounds, enables *Cladonia* to become pre-eminent. Further, on the disintegration of a lichen cover of mixed *Cetraria* and *Cladonia* it is the *Cetraria* which reasserts itself more quickly.

The two chief higher plants *Festuca ovina* and *Agrostis* spp. provide an interesting contrast in growth form and behaviour. Both gain a footing in the Bare stage from surviving parts fallen from the eroding dune face, but whereas *Festuca* is widespread, *Agrostis* is strictly localized and sporadic, surviving only in large sods and in the absence of exceptional droughts. Moreover, *Festuca* reproduces by seed, wet summers favouring the survival of the seedlings, while *Agrostis* does not. Thus the tussock fescue is generally scattered whilst the stoloniferous *Agrostis* spreads from a few nuclei.

The behaviour of *Festuca* and *Agrostis* and the relationships between them are bound up with the presence of a lichen cover, particularly of *Cladonia silvatica*. The individual fescue tussock lives long, probably 20–30 years, increasing in size with age, but eventually dies away in part, becoming resolved into a number of smaller units. How far this behaviour is the outcome of internal readjustments between marginal and peripheral shoots and how far it is due to the influence of *Agrostis* or *Cladonia* or both is not known, but the net result in the successive waves is a reduction in the average size of the fescue plant, an increase in number of individuals and a reduction in cover

Table XI. *Comparison between the number, size and cover per cent of* Festuca ovina *in the* Festuca *and* Agrostis *"streams" in the Early, Middle and Late stages of the succession*

	No. of fescue plants per 1 sq. m.	Cover %	Av. area of plant in sq. cm.	No. of fescue plants per 1 sq. m.	Cover %	Av. area of plant in sq. cm.
	Festuca "stream"			*Agrostis* "stream"		
Early stages	24·3	7·4	31·2	10·4	2·5	24·0
	Averages of data for the *Polytrichum*, *Cetraria* and *Cladonia-Cetraria* stages (Table IV)			Averages of data for the *Agrostis* patches in the *Cladonia-Cetraria* and *Cladonia* stages (Table VIII)		
Middle stages	52	6·9	13·6	27	2·5	9·0
	Festuca society			*Agrostis* society		
Late stages	86	2·6	3·0	86	2·6	3·0

per cent. This is seen in Table XI where the data for the *Festuca* and *Agrostis* stream are separated. The two groups form an interesting comparison both in vertical and horizontal series, the vertical showing trends in the sere as a whole, the horizontal the change taking place in the *Festuca* stream with the spread of *Agrostis*. In the vertical series the two streams are alike in the increase in number and the decrease in average size of the individual plants as development proceeds; they are unlike in that in the *Festuca* stream there is a decrease in cover per cent, whilst in the *Agrostis* stream the cover per cent remains constant. In the horizontal series, recording (in the Early stages at least and probably in the Middle stages) the change in the *Festuca* following the spread of *Agrostis*, comparison shows the reduction in values in all three categories and a clear trend in the direction of the values found in the Adult stage.

A continuously changing relationship between *Festuca* and *Agrostis* ending in a static relation offers a simple explanation of the structure of the Adult stage. But the process cannot be a continuous one in the sense that it starts and proceeds continuously with slow change towards an equilibrium reached only in the Adult stage, for periodic retrogression and disruption intervenes. What is shown is the tendency in each stage towards an equilibrium reached perhaps only in the Adult stage, where, as in earlier stages, the origin of some fescue individuals by splitting is obvious. The evidence suggests that while the Middle stages may approach the *Festuca-Agrostis* relationship found in the Adult stage, yet the Adult stage cannot be derived directly from it. The most likely origin of the Adult community is to be sought rather in some of the retrogressive communities of the Middle stages, where an incomplete disintegration and denudation, followed by fresh colonization by fescue seedlings and by a relatively speedy development of the *Cladonia* carpet, would account for the phenomena presented.

Although the full developmental change has not been observed, there is more evidence to bridge the gap between the Early stages and the *Festuca* and

Agrostis societies of the Middle. It is clear that the *Festuca* and *Agrostis* societies are not merely later stages of the *Cladonia-Cetraria* stage with *Festuca* and the *Agrostis* patches respectively of the Early stages; for retrogression sets in in both. Moreover, the spread of *Agrostis* centrifugally from the *Agrostis* patches converts the *Cladonia-Cetraria* carpet into one of *Cladonia* alone and brings about a marked reduction in the cover per cent of fescue. The origin of the *Agrostis* and *Festuca* societies, it seems to me, must be sought in intermediate degenerate phases of the *Agrostis* patches and in the *Cladonia-Cetraria* with fescue in which retrogression has been arrested before any or much soil erosion has taken place and a fresh start in rebuilding is made by the redistributed surviving components. Communities of this kind have been described. Thus the degenerate *Agrostis* patches exposing bare soil between its scabs of lichen in which *Cladonia* and *Cetraria* have much the same values as in the *Cladonia-Cetraria* stage (Table VIII, p. 20), have scattered *Agrostis* and *Festuca* with 8·6 plants per sq. m., each plant of an average size of 29·2 sq. cm. together covering 2·5 % of the area. The surface soil has an average humus content of 0·96 %. Herein are the makings of the *Agrostis* society, for an increase in the number of *Agrostis* shoots would be accompanied by the same kind of change as occurs in the *Cladonia-Cetraria* stage by invasion from an *Agrostis* patch. Indications of the change are seen by a comparison of the data from two stages in rebuilding (Table VIII).

Similarly the *Festuca* society appears to be derived from the partially degenerate *Cladonia-Cetraria* stage in which an incomplete lichen cover mainly of *Cetraria* is studded with *Festuca* now freed from its besetting ruff of *Cladonia*. The data for the fescue show larger plants covering 7·1 % of the area and the humus content of a partly eroded patch is 1·19 %. Invasion by *Agrostis* would find well-established *Festuca* and *Cetraria* in possession and it would take longer to reach the *Festuca-Agrostis* relationship found in *Agrostis* patches. This would explain the 6·9 % cover of fescue in the *Festuca* society and the higher cover per cent of *Cetraria* than is found in the *Agrostis* society. There is no evidence that the *Festuca* society develops directly into the *Agrostis*; retrogression prevents that.

In the development of both these societies the numbers of fescue could be increased both by splitting and by fresh colonization so long as bare soil was exposed.

If this interpretation is correct then the later stages are built up out of the disintegrated remains of the preceding on incompletely or scarcely eroded soils.

The significant feature about *Agrostis* is the change in the number of shoots per unit area. The changes are not due to a continuous increase from the Bare stage to the Adult but to a series of rises to maxima and falls from them associated with progressive and retrogressive phases of the vegetation. After each maximum there is commonly a heavy mortality, in some places

100%, beginning in the centre of a patch and working outwards followed by the disruption, partial or complete, of the *Cladonia* carpet. The survivors then begin building up anew. This cycle of change in *Agrostis* numbers is intimately bound up with the development of the lichen mat of *Cladonia silvatica*, clearly shown for example by a comparison between the data for the younger and older (peripheral and central) parts of the *Agrostis* patch in the persisting *Cetraria* stage. While the number of *Agrostis* shoots falls from the margin to the centre (from 74 to 49) the cover per cent of *Cladonia* rises from 30 to 72. There is however no absolute relation between the death of *Agrostis* and either the cover per cent of *Cladonia* or the thickness of its carpet. Clearly if the relation is causal it is so in part only.

The data for *Agrostis* in Table VIII, p. 20, show the rise and fall, but the high number in the Bare stage calls for some comment. When a sod falls it may bear a high number of *Agrostis* shoots; commonly the number is small and increases as the *Agrostis* patch passes back across the Bare stage. The high number (146) given is partly explicable on this basis but it is also partly due to close rabbit grazing and to the stimulus to shoot production of the fresh deposit of sand.

The cause of the cyclic change is clear enough in the moss-lichen succession where the lichen carpet disintegrates following the decay of the anchorage provided first by living, later by dead *Polytrichum* shoots. But it is not at present clear why the number of *Polytrichum* shoots should decrease on a stable soil nor why *Agrostis* should pass through these cycles of change. The causes are obscure and will not be discussed until further work is done. But lest a wrong impression is given it may be as well to state now that the phenomenon is independent of climatic cycles inasmuch as retrogression and progression take place simultaneously. At the same time their relative rates may be affected. Thus as the drought continued retrogression became more and more pronounced; the Bare stage widened, the *Agrostis* patches in the Bare stage died, the *Polytrichum* stage widened at the expense of the *Cetraria* stage which was almost obliterated, and disruption of the *Cladonia-Cetraria* and *Cladonia* stages proceeded rapidly. But the change from drought to much rain failed to check retrogression as the following numbers per 1 sq. ft. in the *Agrostis* society of the Middle stages show: in the years 1934, 1935 and 1936 the numbers were 223, 70 and 1 respectively. And the same kind of change takes place in the absence of rabbits. The primary causes therefore seem to lie in the community itself and its soil relationships.

Summary

The origin and development of a *Festuco-Agrostidetum* is described from an area of infertile sand. For the most part the species are the same in the different stages of the succession but an adequate descriptive and differentiating

basis is afforded by the statistically determined frequency (dispersion) and cover per cent. *Polytrichum piliferum* is important as pioneer and accumulator of blown sand, lichens are fairly numerous and two of them, *Cetraria aculeata* and *Cladonia silvatica*, play leading parts, while higher plants are few, the most important being *Festuca ovina* and *Agrostis alba* and *A. tenuis*. The species of *Agrostis* behave in the same way and are considered together. In a neighbourhood characterized by its richness in annual plants it is in keeping with the poverty of the soil that only the least exacting species—*Aira praecox* and *Teesdalia nudicaulis*—are found.

The sere is described in three parts, the Early, Middle and Late stages. The main point of interest emerging from the study is that there is no continuous progression up the inclined plane of seral development from the simple to the more complex community with a corresponding increase in soil organic matter, but that each stage consists of a series of progressive and retrogressive phases separated by a peak stage. The succession in short is wave-like or cyclic.

The Early stages begin with a Bare stage at the foot of eroding dune. Here erosion takes place until an erosion pavement checks further removal of sand. Marginal invasion by *Polytrichum piliferum* leads to its dominance and sand accumulation for which this species is well adapted. On this thin blanket of stable sand there follow stages dominated respectively by *Cetraria aculeata*, and a mixture of this species with *Cladonia silvatica*. Under the mat of mixed *Cladonia-Cetraria*, *Polytrichum* dies and the mat, having lost its anchorage, disintegrates in whole or in part, exposing the soil to partial erosion or in the extreme case to complete erosion down to the erosion pavement. On the erosion pavement the cycle begins again: *Polytrichum* invaders afford anchorage for *Cetraria* which forms an almost continuous mat, and owing to the lack of blown sand *Cetraria* may remain dominant for many years.

Further development of the vegetation is conditioned by the presence of higher plants. *Festuca* and *Agrostis*, the former scattered but widely distributed, the latter in patches and sporadic, become established vegetatively (*Festuca* in favourable seasons by seed) in the Bare stage from surviving parts brought down from the eroding bank. These pass back, so to speak, through the stages of the moss-lichen succession. Their general effect is to expedite the progressive succession and carry it a stage further to the dominance of *Cladonia silvatica*. But their influence is local, that of *Festuca* being confined to a narrow ring round the tuft, that of *Agrostis* to the patch of soil it occupies. At this stage of development the crest of the wave consists of patches of *Agrostis* in a mat of *Cladonia*, set in a background of *Cladonia-Cetraria* studded with scattered *Festuca*.

The crest of the next wave (Middle stages) is also patchy: patches of abundant *Agrostis* and relatively few *Festuca* are set in a background with few *Agrostis* but many *Festuca*. Both have an almost continuous carpet of *Cladonia*.

The crest of the Late stage is an intimate mixture of abundant *Agrostis* and numerous but small *Festuca* again set in a carpet of *Cladonia*.

None of these peak stages is stable; the *Agrostis* dies in whole or in part and the lichen carpet disrupts, leaving the soil open to erosion. A series of stages, retrogressive from the peak of the Middle stages, is described. Retrogression also takes place from the peak of the Late stage but no data are presented.

The succession on the erosion pavement has not been followed out. The succession described is on blown sand and evidence is adduced to show that the crests of the Middle and Late stages are built up out of the retrogressive, partially disintegrated communities of the Early and Middle stages respectively.

The relationships between *Festuca* and *Agrostis* are described for each of the three stages. It is shown that where *Agrostis* invades a lichen community with *Festuca*, *Cladonia* becomes dominant and the number and size and therefore the total area covered by *Festuca* decreases. It is also shown that from the Early to the Late stages the numbers of *Festuca* increase but the size of the individual decreases. The cover per cent of *Festuca* in communities with abundant *Agrostis* tends towards the relatively constant and low figure of 2·5. There is in each main stage a progression towards this apparent equilibrium which fails of achievement because the community disintegrates before it is reached. Even in the Late stage dying out of *Agrostis* occurs.

The cyclic behaviour is discussed. It is shown that while a series of dry years speeds up retrogression relatively to progression both stages exist side by side, and that while climate holds the balance, now favouring one, now the other, the periodicity is inherent in the vegetation itself and connected in some way with the lichen cycle. This is regarded as a partial cause: the primary cause remains obscure.

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VEGETATION OF GRASS VERGES AND OTHER EXCESSIVELY TRODDEN HABITATS

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The vegetation of the grass verge, whether it occurs as a mere strip along the roadways of this country or whether it borders the wide stock routes of the hinterland of Australia (Davies, 1933), is always of considerable interest. Its careful study under properly controlled conditions may prove important in the ecological consideration of plant communities as well as in the study of ecads. There appears to be a considerable degree of similarity between the vegetation of the trampled grass verge bordering on highways and that of the grassy footpath or the sheep track, whether in the lowlands or at high elevations. Gateways providing the means of access to fields provide other interesting material for study. The very sameness exhibited in the botanical composition of these plant communities would lead one to enquire whether or not certain basic principles in ecological distribution are therein involved. The data presented in the present paper are drawn from British examples, but these could be supported by notes and observations made in other countries, particularly Australia and New Zealand (Levy & Davies, 1930).

The close similarity shown by the ecological distribution around gateways and footpaths is so well marked over a wide range of climatic and edaphic conditions that it becomes important to trace the factors concerned in this distribution. Even within the confines of Great Britain differences due to climatic, topographical and edaphic influences will be apparent from centre to centre. Bates (1935) has drawn attention to the nature of the footpath vegetation, and suggests that the treading and puddling of the soil, especially during the winter months, lead to the crushing of vegetation under foot and hoof, and that this is best withstood by certain cryptophytic elements in the vegetation.

There can, of course, be no doubt that treading as such has in itself a considerable influence upon the character of the vegetation of a grassy pathway, but it is likely that a number of factors, complex in their interaction, are involved. In the first place the foot or hoof action is not merely one of direct pressure from above. Thus in the case of treading by humans, the vertical pressure is accompanied by a distinct horizontal and semi-rotary twist as the ball of the foot leaves the ground. There is a somewhat analogous action by the grazing animal. These actions tend to break the ground, move, and therefore aerate, the soil and help to earth up the base of the plants. So long

as disturbance is not too frequent, therefore, treading *qua* treading helps to benefit the majority of grassland plants. As the frequency of treading increases, however, its influence becomes proportionately selective, and if taken to the extreme only an ephemeral vegetation (if any) will survive. The prevalence of *Poa annua* under conditions of over-treading is brought out in the present article. This grass, though not a characteristic ephemeral, is relatively short-lived[1] and shows an amazing capacity to flower, set seed and re-establish itself.

The plants most commonly associated with the grass verge in lowland Britain are *Lolium perenne* and white clover (*Trifolium repens*). Agriculturally these are among the most useful of our pasture plants, and for that reason a good deal is known about their behaviour. Under a reasonably high standard of soil fertility and under pasture conditions they blend together. They require to be grazed on a fairly short rotation. Their presence as dominants on the footpath or grass verge situated among fields of *Agrostis* would indicate a higher standard of fertility on the footpath or verge than on the surrounds. Many graziers maintain that farm animals prefer to feed upon these tracks and footpaths, and if this is so, such a concentration of stock would cause a building up of soil fertility. The tendency for stock to concentrate upon certain areas is strikingly borne out when the grazings found on each side of moorland roadways are considered. The sheep concentration along these strips has been stressed by Stapledon (1935). On the basis of their botanical composition alone a heavier stock carrying capacity would be expected of them when compared with the average of the adjoining moorland grazings. Added fertility and the consequent concentration of stock have probably, therefore, a determining influence upon the flora of road verges, footpaths and gateways.

It is becoming increasingly clear that the grazing animal plays a fundamental part in determining the floral composition of the grassland upon which it browses. This feature is well shown by the results obtained in one of the pasture experiments (E 155) conducted at Aberystwyth. An area of land was sown down in the spring of 1933 with an experimental seeds mixture. Various plots laid upon it have subsequently been subjected to different intensities of stocking (as measured by the amount of time spent on each by grazing animals). Where the animals have been left for the longest time the pasture now consists mainly of perennial rye-grass, white clover and *Poa trivialis*. Where stock have been concentrated during the spring and summer, and the pasture has been rested in the autumn and winter, the herbage now consists almost entirely of cocksfoot (*Dactylis glomerata*). On another plot from which

[1] There is some evidence to suggest that *P. annua* is not a typical therophyte in Raunkiaer's sense (1934). In cases where it is "earthed up" (as on a frequently trodden path, or on a golf green which is periodically dressed with sand, earth or compost) *P. annua* produces "runners" which live for more than one year, and from the nodes of which new tillers together with new roots are borne. *P. annua*, therefore, should be classed as a hemicryptophyte in company with the majority of the species of British pastures.

hay has been removed, and which has been heavily grazed during both the pre- and post-hay periods, the present sward is made up chiefly of daisies (*Bellis perennis*) and certain inferior grasses. This last plot has been sown with commercial seeds, while the two others were sown with pedigree strains—products of the Welsh Plant Breeding Station. This need not, however, concern our present theme, although the point is one of fundamental importance with regard to the general problems of grassland improvement. The point to note is that the total amount of treading on all of these plots is considerable, and yet the herbage on one series is now *Lolium*-white clover; on another *Dactylis*, and on still another *Bellis*.

The vegetation found on footpaths and verges around Aberystwyth has been carefully observed over a number of years. The general evidence shows that where the ground is made very bare during periods of heavy traffic, *Poa annua* tends to dominate; where there is rather less traffic *Lolium* and white clover will be dominant, but *Cynosurus*, *Agrostis*, *Holcus* and a number of other species will enter into the majority of these swards. *Poa pratensis* is not a frequent constituent, though it may often be found in the longer grass of the surrounding hedgerows which are normally not trodden upon and only lightly grazed in most seasons.

Botanical material and technique

The botanical evidence under consideration in this paper has been taken from different parts of the country, the percentage cover method (Davies, 1931) being employed for sward analysis. Table I shows the average composition of grass verges at the following centres:

A. Lowlands	B. Uplands
Cardiganshire (Aberystwyth)	Montgomeryshire (Lake Vyrnwy)
Derbyshire (Buxton)	Devon (Brendon Common I)
Yorkshire (Great Smeaton)	Devon (Brendon Common II)
Northumberland (Alnwick I)	Roxburghshire (Carter Bar)
Northumberland (Alnwick II)	Denbighshire (Cader Benllyn)
Somerset (Barle Valley)	Denbighshire (Conway Valley)
	Merionethshire (Bwlch-y-Groes)

The road verges examined have in all cases been transected from the carriage way outwards (i.e. away from it). There is an evident relationship between the sharpness of zonation on these verges and the quantity of foot traffic (including farm stock) using them. Therefore we find that some grass verges will exhibit little or no zonation while upon others zonation is very striking. In most cases, however, the very narrow strip directly against the roadway is distinctly marked, and on it (lowland situations) *Lolium* is usually the most abundant grass. The average figure of 33% for *Lolium* on lowland verges (Table I) gives a reasonably true picture of its importance in the road "edge" community. *Agrostis* and white clover (*Trifolium repens*) are on the average less abundant than *Lolium*, and are followed in order of abundance

by *Poa annua* and the fine-leaved fescues (*Festuca*). *Poa pratensis*, *Bromus*, *Alopecurus*, *Dactylis* and *Holcus* also occur, but individually they are seldom abundant.

Table I. *The average composition of* 13 *grass verges along roadways in lowland and upland situations in Great Britain*

	Lowlands (fenced roadways)			Uplands (unfenced moorland roads)		
Species	Edge*	Middle†	Inner‡	Edge*	Middle†	Inner§
Lolium perenne	33	20	4	6	1	—
Poa annua	9	—	—	29	Trace	2
Agrostis (usually A. tenuis)	15	21	19	25	48	24
Holcus (lanatus et mollis)	2	10	21	—	—	3
Trifolium repens	14	7	3	9	3	2
Festuca (rubra et ovina)	6	7	8	7	19	22
Dactylis glomerata	3	7	20	—	—	—
Poa pratensis	—	5	4	—	1	—
Nardus stricta	—	—	—	6	1	11
Molinia caerulea	—	—	—	—	Trace	—
Other species	18	23	22	17	27	36
Total	100	100	101	99	100	100

* Usually first 1½–2 ft. from edge of carriage-way.

† Zone roughly 2–5 ft. from edge of carriage way.

‡ Zone from about 5 ft. from edge of carriage way and to fence or base of hedge.

§ The strip of open moorland about 2 yd. wide lying between the "middle" zone and the moorland proper.

Comparing the data for "edge" in the uplands and lowlands (see Table I) it is apparent that white clover and the fine-leaved fescues occur in both, while *Nardus* only finds a place in the upland roadside community. The most striking difference between lowland and upland, however, is the change over from dominance of *Lolium* to dominance of *Agrostis* and *Poa annua*. This difference is probably connected with the relative standard of soil fertility associated with the two habitats.

The "middle" zone under lowland conditions shows a decrease in the proportion of *Lolium* and an increase in *Agrostis*, *Holcus* and *Dactylis*. *Poa pratensis* occurs in this zone, but *P. annua* is absent. This is to be expected because there is less treading and consequently less bare space formed for the establishment of *P. annua*. *Agrostis*, *Holcus* and *Dactylis* will normally thrive better relatively to *Lolium* where soil fertility is lowered. The "middle" zone on the uplands shows similar trends. *Lolium* has almost disappeared; there is a sharp increase in both *Agrostis* and *Festuca* as well as in the more typical moorland species.

Considering the "inner" zone in the lowlands there is a significant increase in *Dactylis* and *Holcus* accompanied by a decrease to negligible proportions of both *Lolium* and white clover. *Poa annua* does not enter into the community, but *P. pratensis* occurs. This zone will normally not be grazed nor trampled to any extent. Usually it will be mown by roadmen once or twice during the

active growth period and quite often the herbage then cut will be left *in situ*, or may be collected into heaps and later carted away. Associated species commonly met with in this zone are *Arrhenatherum elatius*, *Trisetum flavescens*, *Agropyron repens*, *Deschampsia caespitosa*, *Rubus fruticosus* and members of other families, including in particular the Umbelliferae and the ferns.

The "inner" zone on the mountain roads approaches in botanical composition the better class of ordinary hill pasture. *Agrostis* and *Festuca* are dominant with an increased percentage of *Nardus* compared with the outer verges. The other moorland plants, particularly *Calluna vulgaris*, *Vaccinium Myrtillus*, *Galium saxatile* and *Potentilla erecta*, take a prominent place in these communities, as also do certain mosses and lichens. Species more typical of lowland pastures may also occur, and these include *Achillea Millefolium*, *Plantago lanceolata*, *Ranunculus repens*, *Bellis perennis*, *Sagina procumbens*, *Hypochoeris radicata* and *Prunella vulgaris*. It will be noted that *Poa pratensis* takes practically no part in the average composition of the hill roadside associations. It is also noteworthy that *Molinia caerulea*, which is among the most abundant elements of the grass moor vegetation in Britain, takes virtually no place in the flora of the roadside habitats. Experiments at Aberystwyth have shown that frequent defoliation can be extremely harmful to *Molinia* (Stapledon & Thomas, 1930).

The vegetation of particularized road verges

The evidence discussed below will illustrate the considerable range of variation which is found in the composition of characteristic road verges occurring in different situations. Usually *Lolium* takes a more prominent place on the verges of the better grazing than of the poorer districts, as was noted in the remarks on Table I. These data were collected from the following districts:

(1) *Northumberland* (*near Alnwick*). Representative of land which carries high-quality pastures and in which cattle will fatten on summer grass. *Lolium* a prominent constituent of most pastures.

(2) *Cardiganshire* (*near Aberystwyth*). Representative of the cattle-rearing pastures of Western Britain. Old grasslands, mainly *Agrostis*, with white clover and *Holcus*. *Lolium* usually contributes less than 5% to the herbage of these pastures.

(3) *Roxburghshire* (*Carter Bar*). Typical good quality Cheviot grazings; in these *Agrostis* and *Festuca* are the chief grasses and there is some white clover, and occasional plants only of *Lolium*.

(4) *Montgomeryshire* (*Lake Vyrnwy*). Open hill sheep grazings on which *Festuca* is dominant. There is some *Agrostis*, but white clover and *Lolium* are both absent.

(5) *Denbighshire* (*Cader Benllyn*). Open hill moorland on which *Nardus* dominates.

(6) *Devonshire* (*Brendon Common near Exmoor*). Typical dry moor with *Calluna* as the dominant and *Vaccinium* the most abundant associate.

These centres show examples, therefore, of a range of dry land associations from the *Lolium* and *Agrostis* types at the one extreme, to *Nardus* and *Calluna* moorland at the other. At each centre transects have been made from the roadway outwards, i.e. towards the fence or hedge of enclosed roads, and to the open hill grazing where the roads are unfenced.

Table II. *Northumberland. Road verge vegetation* 5 *miles north of Alnwick and on main road. Three zones outward from carriage-way:* (*a*) 0–1 *ft.*, (*b*) 1–3 *ft.* *and* (*c*) 3–6 *ft. on to base of hedge. Percentage area. Analysed* 19. ix. 34

Species	(*a*) 0–1 ft.	(*b*) 1–3 ft.	(*c*) 3 ft. to hedge
Lolium perenne	65	20	5
Dactylis glomerata	10	20	30
Agrostis tenuis *et al.*	—	20	15
Festuca rubra *et al.*	—	10	10
Poa pratensis	—	10	10
Holcus mollis	—	5	20
H. lanatus	—	—	5
Trifolium repens	20	5	Trace
Other species	5*	10†	5‡
Bare ground	Nil	Nil	Nil

* Chiefly *Achillea Millefolium*, *Potentilla Anserina*, *Chaerophyllum temulum*.

† Chiefly *Chaerophyllum temulum*.

‡ Chiefly *Chaerophyllum temulum*, *Anagallis arvensis*, *Achillea Millefolium* and *Urtica dioica*.

The data given in Table II show an interesting transition from road to hedge; *Lolium* and white clover decrease rapidly from zone (*a*) to (*c*), whereas *Dactylis*, *Agrostis* and *Holcus* show corresponding increases. *Festuca* and *Poa pratensis* each occur away from the carriage-way, but not in zone (*a*). *P. annua* was not recorded at this centre.

Table III. *Cardiganshire. Road verge vegetation* 2 *miles north of Aberystwyth and on main road. Four zones outward from carriage-way to hedge base:* (*a*) 0–2½ *ft.*, (*b*) 2½–4 *ft.*, (*c*) 4–7 *ft.*, (*d*) 7–9 *ft. on to hedge base. Percentage area. Analysed* 11. iii. 37

Species	(*a*) 0–2½ ft.	(*b*) 2½–4 ft.	(*c*) 4–7 ft.	(*d*) 7–9 ft.
Lolium perenne	25	40	5	5
Agrostis tenuis *et al.*	—	5	35	25
Poa annua	40	15	Trace	—
Holcus lanatus	—	5	30	40
Trifolium repens	20	15	5	Trace
Bellis perennis	15	10	5	—
Plantago lanceolata	—	5	10	3
Other species	—	5*	10†	27‡
Bare ground	95	30	20	Nil

* *Trifolium dubium*.

† *T. dubium*, mosses, *Crepis*, *Rumex*, *Bromus*.

‡ *Dactylis glomerata* (5 %); *Poa pratensis* (5 %); *Cynosurus cristatus* (5 %); *Festuca rubra* (7 %); *Arrhenatherum avenaceum* (2 %); *Rumex obtusifolius*, *Chaerophyllum temulum*, *Rubus fruticosus* (3 %); *Sonchus oleraceus*.

The data given in Table III are from near Aberystwyth. Zone (*a*) does not rightly belong to the grass verge community, but forms part of the carriage-way proper. This strip is frequently used by wheeled traffic, although not a part of the tar-macadam road surface. *P. annua* is the most abundant species in this zone. On the grass verge proper *Lolium* is dominant in the well-trodden zone (*b*), whereas *Agrostis* and *Holcus* together form the bulk of herbage in the other two zones. There is a decline in the proportion of white clover and also of *Bellis* from the roadway to the hedge. *Poa pratensis* takes no part in zones (*a*), (*b*) and (*c*), but contributes about 5% to the herbage cover in (the infrequently trodden) zone (*d*). It is here in association with typical thicket and hedgerow species, including *Dactylis*, *Festuca*, *Arrhenatherum*, *Rubus* and *Chaerophyllum temulum*.

Table IV. *Roxburghshire. Road verge communities on the Cheviots near Carter Bar (main road south from Jedburgh). Four zones outward from roadway to open hill:* (*a*) 0–1½ *ft.*, (*b*) 1½–4½ *ft.*, (*c*) 4½–7½ *ft.*, (*d*) 7½–30 *ft. and merging to open hill. Percentage area. Analysed* 19. ix. 34

Species	(*a*) 0–1½ ft.	(*b*) 1½–4½ ft.	(*c*) 4½–7½ ft.	(*d*) 7½–30 ft.
Lolium perenne	45	15	Trace	—
Agrostis tenuis *et al.*	10	10	50	60
Poa annua	3	—	—	—
P. trivialis	10	Trace	—	—
Trifolium repens	25	25	10	5
Festuca rubra *et al.*	—	—	25	20
Cynosurus cristatus	5	25	—	—
Bellis perennis	Trace	12	—	—
Other species	2*	13†	15‡	15§
Bare ground		Not recorded		

* Chiefly *Achillea Millefolium* and *Plantago lanceolata*.

† Chiefly *Ranunculus repens*.

‡ Including mosses (5%), *Deschampsia caespitosa* (5%), *Molinia caerulea* (5%), and traces of *Holcus lanatus* and *Anthoxanthum odoratum*.

§ Including *Deschampsia flexuosa* (5%), mosses (2%), *Juncus communis* (2%), *Holcus lanatus* (2%), *Carex* (2%) and traces of others.

The evidence in Table IV exhibits the same general trends as before. Although these data are from elevated country (about 1000 ft.) on the Cheviot Hills the narrow strip of vegetation nearest the road proper (Zone (*a*)) consists chiefly of *Lolium* and white clover. Transecting outwards from the roadside both these plants become less abundant, and are replaced by *Agrostis* and *Festuca*, which become completely dominant on the adjoining hill grazing, although white clover is shown to be still present in small amount. *Poa annua* and *P. trivialis* were recorded, but were not abundant even in Zone (*a*) nearest the roadway, while *P. pratensis* did not occur. Among the forbs *Bellis* is the chief contributor, occupying 12% of Zone (*b*). The prominence of *Cynosurus* in Zone (*b*) is particularly interesting for this species is among the more promising of our grasses in connexion with the improvement of hill pastures.

Table V. *Montgomeryshire. Road verge communities above Lake Vyrnwy. Four zones outward from unfenced mountain road as follows: (a)* 0–1½ *ft., (b)* 1½–3 *ft., (c)* 3–4½ *ft., (d)* 4½–30 *ft. merging to open hill. Percentage area. Analysed* 13. ix. 34

Species	(*a*) 0–1½ ft.	(*b*) 1½–3 ft.	(*c*) 3–4½ ft.	(*d*) 4½–30 ft.
Agrostis tenuis *et al.*	45	70	30	28
Poa annua	10	5	—	—
Trifolium repens	20	5	Trace	Trace
Festuca rubra et ovina	20	20	65	54
Other species	5*	Nil	5†	18‡
Bare ground	5	3	Nil	4

* *Lolium perenne, Deschampsia caespitosa, Cynosurus cristatus, Bellis perennis* and *Plantago lanceolata.*

† Mosses and *Cynosurus cristatus* chiefly.

‡ *Galium saxatile* (9 %), *Luzula campestris, Potentilla erecta, Viola lutea* and mosses.

The data embodied in Table V are from a roadside at an elevation of approximately 1000 ft. in a typical sheep-grazing district of Central Wales. The surrounding moorland vegetation is siliceous grassland (*Festuca* with *Pteridium*).

The road verges are, however, conspicuously free from bracken. Comparing the botanical evidence with that of Tables II–IV, the outstanding feature of Table V is the complete absence of *Lolium* in all zones except that nearest the roadway. Even here its contribution is negligible. White clover, however, takes a prominent place in the narrow Zone (*a*), but diminishes rapidly in amount as one passes away from the road. *Agrostis* and *Festuca* are the chief plants in all zones, and it is the relative proportion of these two grasses and of white clover which accounts for the main contrast between the several zones under discussion. *Poa annua* is fairly abundant on the road edge, but *P. pratensis* and *P. trivialis* are both absent. Other species are unimportant (*Bellis* and *Plantago* were both recorded) except in Zone (*d*) where *Galium saxatile*, and other plants characteristic of hill fescue pastures, are abundant. Proceeding outwards and away from the roadway *Agrostis* gives way to *Festuca* as the dominant grass, much as in the lowland localities *Lolium* was shown to be replaced by *Agrostis, Holcus* or *Dactylis.*

The data shown in Table VI are from an unfenced moorland track at high elevation (1336 ft.) in North Wales. These mountain roads are seldom used by wheeled traffic, and are usually only partly metalled, although a small car can be taken over them at most seasons of the year. The roadside vegetation, however, often shows marked zonation. In the present instance the part nearest the road shows 35 % of bare ground and the vegetation consists chiefly of *Poa annua.* In Zone (*b*) *Agrostis* and *Festuca* dominate, while in Zone (*c*) *Nardus* is the chief single contributor. The marked restriction in number of species as compared with other centres is worth noting, if only because it represents a condition characteristic of the acid moorlands of Wales. It is

noteworthy too that *Poa pratensis* (8%) occurs in Zone (*b*), but not in the other two zones, nor was it found in the typical moorland vegetation away from the roadside.

Table VI. *Denbighshire. Road verge communities at Cader Benllyn Pass* (1336 *ft.*). *Three zones outward from* (*unfenced*) *mountain roadway as follows:* (*a*) 0–1½ *ft.*, (*b*) 1½–9 *ft.*, *and* (*c*) 9 *ft. outwards merging to moor. Percentage area. Analysed* 14. ix. 34

Species	(*a*) 0–1½ ft.	(*b*) 1½–9 ft.	(*c*) 9 ft. +
Agrostis tenuis et canina	—	33	10
Poa annua	95	—	—
Festuca ovina chiefly	—	22	15
Poa pratensis	—	8	—
Nardus stricta	—	6	40
Rumex Acetosella	5	11	—
Achillea Millefolium	—	11	—
Galium saxatile	—	6	10
Other species	—	3*	25†
Bare ground	35	Nil	Nil

* Chiefly *Sieglingia decumbens.*
† Chiefly *Juncus squarrosus* and mosses.

Table VII. *Devonshire. Road verge communities on Brendon Common* (*Exmoor*). *Four zones outward from roadway* (*unfenced*). *Zones* (*a*) 0–1 *ft.*, (*b*) 1–2 *ft.*, (*c*) 2–3 *ft.*, (*d*) 3–10 *ft. Percentage area. Analysed* 28. vii. 35

Species	(*a*) 0–1 ft.	(*b*) 1–2 ft.	(*c*) 2–3 ft.	(*d*) 3–10 ft.
Agrostis tenuis	25	50	50	—
Festuca spp.	10	10	—	10
Trifolium repens	25*	5	—	—
Lotus corniculatus	5	5	—	—
Achillea Millefolium	25	20	20	—
Calluna vulgaris	—	5	15	50
Vaccinium Myrtillus	—	5	5	15
Other species	10†	Trace‡	10§	25‖
Bare ground	Nil	Nil	Nil	10

* Includes red clover (*Trifolium pratense*) (5%).
† *Anthoxanthum* (5%), *Juncus squarrosus, Sieglingia* and *Deschampsia flexuosa.*
‡ *Anthoxanthum.*
§ *Galium* and *Potentilla.*
‖ *Erica cinerea, Juncus squarrosus, Sieglingia* and *Deschampsia flexuosa.*

The data shown in Table VII are from road verges crossing the heather moors of Brendon Common, a few miles north of Simonsbath and of the portion of Exmoor reclaimed by the Knight family (Orwin, 1929). Perhaps the most striking feature brought out by these data is the great prominence of leguminous plants on the road edge. The vegetation is dense and closely matted, and to this the three legumes (white clover, red clover and *Lotus*) contribute as much as 30%, whereas no legumes are to be found in the adjoining heather moor. Under this particular condition it is *Agrostis, Achillea* and white clover which dominate the road verge community. Proceeding from the road out-

wards white clover at first gives way to *Agrostis*—while in Zone (*d*) *Agrostis* is replaced by *Calluna* as the dominant.

The data relating to grass verges presented in the foregoing tables are reasonably typical, and cover a range of grassland types from *Lolium* and white clover pasture lands at the one extreme to *Nardus* and *Calluna* moorland at the other. The point of practical significance brought out by these data is that the road verges often carry a pasture type which, botanically at least, represents grassland of greater agricultural worth than that of the adjoining permanent grasslands. This difference is often particularly obvious on many hillside and moorland grazings. The data show it to be an equally common feature of our lowland highways.

Pathways

Table VIII. *The vegetation of stock tracks and footpaths; six examples*

Pasture type of surrounding grassland and location	1 Stock track on *Lolium-Agrostis* pasture (Northumberland)	2 Footpath (farm stock excluded) across *Agrostis* pasture (Aberystwyth)	3 Stock track on *Agrostis-Festuca* (Somerset)	4 Sheep track on siliceous hill fescue pasture (Cardiganshire)	5 Sheep track across marshy *Molinia* moor (Cardiganshire)	6 Sheep track on dry *Festuca* "*ffridd*" (Cardiganshire)
Lolium perenne	60	58	—	—	—	—
Poa annua	5	2	8	2	—	45
Agrostis	5	16	47	9	6	25
Trifolium repens	20	1	29	—	—	—
Festuca ovina et rubra	—	8	5	53	12	5
Poa pratensis	—	2	Trace	—	—	—
Scirpus caespitosus	—	—	—	—	32	—
Juncus squarrosus	—	—	—	—	12	—
Luzula campestris	—	—	—	—	—	10
Mosses	—	Trace	—	18	26	Trace
Other species	10	13	11	18	12	15

The data in Table VIII are drawn from widely differing situations largely to lay emphasis upon the considerable variation to be found in the vegetation of pathways in different parts of the country. The Northumberland locality (col. 1) represents good-quality grazing land. The second example (col. 2) comes from the Welsh Plant Breeding Station farm, and from a piece of land to which ordinary farm stock have had no access since 1927, when the area was fenced and weather-recording apparatus erected upon a portion of it. No grazing animal, other than an occasional rabbit, is likely to have gained access into the area concerned. *Lolium* is the chief pathway constituent in both these places, although grazing animals use the one and are excluded from the other. Thus it would seem that the factor of defoliation by grazing as such is not one of importance in the determination of the botanical composition of the pathway.

Three of the other localities are open hill grazings in Wales, and it is noteworthy that *Agrostis*, *Festuca* and such non-gramineous elements as

Scirpus caespitosus and mosses may all be among the major contributors on individual pathways. The dominant plant on any given stock track will, therefore, depend in part upon the degree of treading, but also in part upon the general standard of soil fertility. Thus on lowland pathways (localities 1 and 2) the tendency is for *Lolium* to become dominant, whereas at higher elevations and on poorer soils *Agrostis* and *Festuca* will tend to dominate. *Poa annua*, on the whole, seems to occur more frequently as the dominant contributor on the moorland stock tracks and in other situations of low soil fertility than it does on better soils.

Gateways

Road verges and pathways having been considered it remains to discuss briefly the gateway vegetation, with particular reference to gateways in frequent use by ordinary farm stock. The general orientation of the zones around a well-used field gateway (lowland condition) is as follows:

(i) Immediately about the gate itself is an area completely trodden over and more or less bare of vegetation. In Wales *P. annua* is characteristically present, and is often the only plant recorded.

(ii) In the next zone treading is less severe and the community is usually one in which *Lolium* occurs in fairly large clumps. White clover is nearly always present, and so also is *Poa annua.*

(iii) In the third zone *Lolium* and white clover may be co-dominant but usually in association with a number of other species, providing a mixed pasturage. This zone will normally merge gradually into the general vegetation representative of the body of the adjoining pasture or meadow.

Perhaps the most striking feature of the gateway vegetation again is its similarity from situation to situation. The general orientation seems to be fairly typical under lowland conditions in Britain; a zone in which *Poa annua* is a conspicuous element, then one of tussocky *Lolium* merging into an intimate blend of *Lolium* and white clover, and thence merging gradually into the vegetation of the field itself. In the uplands, where edaphic and other conditions are normally less favourable, *Poa annua* again occupies this "most-trodden" zone, but the next zone is characteristically dominated by *Agrostis tenuis* which merges gradually into *Agrostis* with *Festuca*, and thence into *Festuca* and other hill vegetation. Where white clover appears at all under these hill conditions it is usually in association with *Agrostis*. This is in itself worthy of note and may prove significant in connexion with hill reclamation work.

Summary

1. The vegetation found on certain roadside verges has been studied and the results presented. Observations have also been made on the vegetation of footpaths, stock tracks and around gateways.

2. These several habitats have a good deal in common as measured by the zonation of the vegetation found associated with them.

3. Under lowland conditions in Britain *Lolium perenne*, *Trifolium repens* and *Poa annua* appear to be the most abundant species found on the more heavily trodden part of the road verge or pathway.

4. Under conditions of lower soil fertility, such as those normally associated with heather and other moorland vegetation, the most abundant constituents of the road verge habitat are *Agrostis tenuis*, *Poa annua* and the fine-leaved fescues.

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SOME IMPORTANT COMMUNITIES OF WARM TEMPERATE RAIN FOREST AT MAGAMBA, WEST USAMBARA, TANGANYIKA TERRITORY

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(*With a Map and a Successional Diagram*)

CONTENTS

INTRODUCTION

THE observations on which this paper is based were made in the latter half of 1934 whilst carrying out a 10% strip enumeration survey of the Magamba Camphor Forest, West Usambara, Tanganyika Territory. Briefly, the method

employed consisted of cutting parallel lines through the forest, at first 440 yd. apart and then only 330 yd., and enumerating the forest along these lines to a width equal to one-tenth of the distance between them. With only three-quarters of a chain (16½ yd.) being measured on each side of the line the officer who was doing the booking could usually tell the natives when they were outside the 16½ yd. mark without having to have it measured, as was often the case when the strip was one chain wide on each side. This narrowing of the strip measured meant increasing the number of lines, but at the same time it gave a better sampling of the forest.

The direction of the lines was chosen so that they ran more or less across the main topographic features. The "major species", which are regarded as being of economic value, were measured down to 3 in. quarter girth (Q.G.), i.e. 1 ft. in girth at breast height, and the other or "minor" species down to 12 in. Q.G. "Timber heights", i.e. the length of bole suitable for conversion to timber, were estimated with the aid of a 15 ft. staff placed against the trees. The number of poles, i.e. trees too small to be measured but thicker than one's wrist, of each major species, and of all the minor species together, and also the number of seedlings of each major species were recorded for every section of 110 yd. along each line. Notes were made of the species forming the second or understorey, the undergrowth (shrubs) and the ground flora, and also on the aspect, slope, density of canopy and topographical features. Readings of an aneroid barometer were recorded every two sections (every furlong) and at every stream and ridge.

The major species were (vernacular (Kisambaa) names first):

Mkulo	*Ocotea usambarensis* Engl.[1]	
Msee	*Podocarpus* sp.[2]	Not recorded separately
,,	*P. usambarensis* Pilg.	
,,	*P. gracilior* Pilg.	
Mkuka	*Ficalhoa laurifolia* Hiern.	
Mkomohoyo	*Pygeum africanum* Hk. f.	
Mbokoboko	*Entandophragma* sp.	
Ngwe	*Olea hochstetteri* Baker	
Mkunguni	*Clausena melioides* Hiern.	

A map (scale 4 in. to 1 mile) has been prepared showing the distribution of ten main vegetation communities and the more important topographic features. The boundaries of the communities were noted in the field books and were plotted across each line on the map; they were then joined up between the lines, due regard being paid to differences caused by changes in the

[1] To avoid constant repetition the authors' names are omitted in what follows; they are given in the full list of plants tabulated in Appendix II.

[2] Originally thought to be *P. milanjianus* Rendle, but now believed to be *P. falcata* or *P. mannii*; possibly all these species are present.

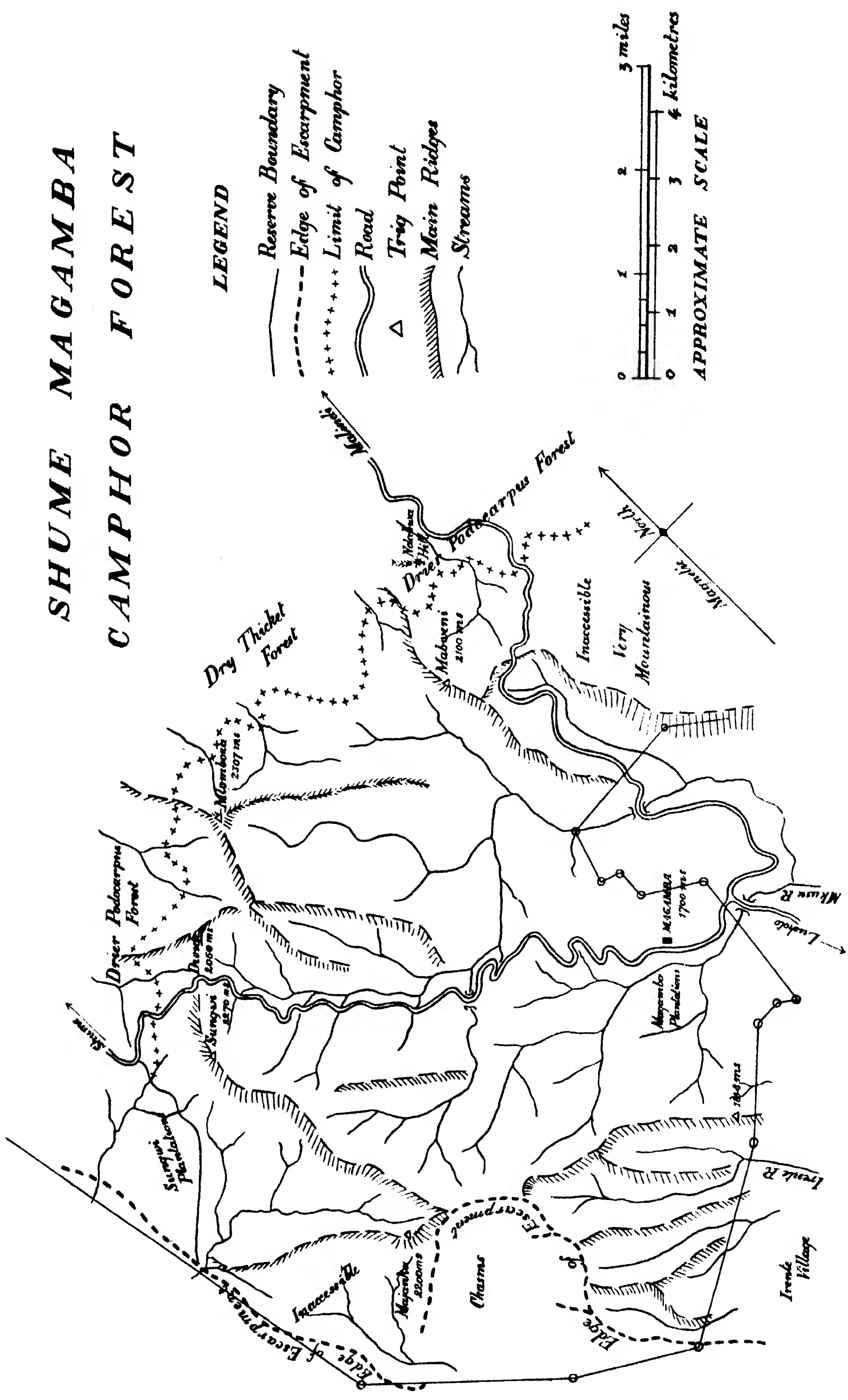

Fig. 1. Sketch map of the Shume-Magamba forest.

topography. The distribution of the communities is too complicated for the map to be reproduced on a smaller scale. A rough sketch-map has, however, been prepared on a smaller scale (p. 52), showing the main topographic features of the region.

Botanical material of nearly all the trees, shrubs and herbs encountered in the course of the work was collected by the writer, and much of it determined and compared by him at the East African Agricultural Research Station, Amani. These determinations were corrected or confirmed, and further determinations made, by Mr A. C. Hoyle of the Imperial Forestry Institute, Oxford.

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TOPOGRAPHY AND CLIMATE

The Shume-Magamba forest reserve (60,900 acres) occupies the western portion of the highlands known as the Western Usambaras. These highlands are situated in the Tanga Province, in the north-east corner of Tanganyika Territory. A very good general account of the Usambaras is given by Moreau (1935).

The Magamba forest (16,500 acres) is really the "camphor" (*Ocotea usambarensis*) or "wet" forest portion of this reserve. Apart from open glades, the remainder of the reserve appears to consist of three main types of vegetation:

(i) "Drier *Podocarpus* forest"—a transitional type with *P. usambarensis* as the dominant species and *Olea hochstetteri* as a common co-dominant.

(ii) "Dry thicket forest"—rather varied in composition, with no trees of timber size and with a thicket undergrowth of various shrubs, including species of *Euclea*, *Myrsine* and *Toddalia*, and *Maba buxifolia*.

(iii) "Dry cedar forest"—*Juniperus procera* dominant.

This paper deals only with the "wet" or "camphor" forest region.

Topography. The country is somewhat broken and the altitude varies from 1615 m. (Irente stream) to 2300 m. (Mlomboza)—5300–7600 ft. All the main

ridges run and increase in altitude more or less from south-east to north-west. The most important ridge runs from above Irente village (near Lushoto) along the edge of the escarpment above the Mazinde railway station to near Majanka "peak" (2200 m.—7260 ft.) and then on to just beyond Sungwi "peak" (2270 m.—7380 ft.). To the west of the ridge between Majanka and Sungwi there is a broad "shelf" with some subsidiary ridges before the edge of the escarpment is reached. This shelf is about 1½ miles wide and varies in altitude from 1900 to 2050 m. (6270–6765 ft.). The northern portion of it, below Sungwi, has been exploited for the Shume sawmill and some of it has been planted up, mainly with conifers—*Juniperus procera*, *Cupressus lusitanica* and *C. macrocarpa*.

The south-western and western edges of the forest lie along the top of the Usambara escarpment, which is from 1500 to 1900 m. (4950–6270 ft.) above the surrounding country. To the north-west, north and north-east the camphor forest merges into the "drier *Podocarpus* forest" or "dry thicket forest". The eastern and southern boundaries adjoin private estates or "public lands"; the latter have been denuded of forest and cultivated by the natives.

Climate. No temperatures have been systematically recorded in the vicinity of Magamba. However, on the open verandah of the forest house (1700 m.—5600 ft.) a thermometer showed a minimum temperature of 37° F. in August. Several nights were spent in camp on forested but rather exposed ridges at about 2100 and 2230 m. (6930 and 7360 ft.), and although very cold there was no actual frost. Frosts, however, are frequent in the valley bottom at Magamba, and they are experienced in the open glades of the dry (cedar) forest at Shume (2100 m.—6900 ft.).

There are two main wet seasons, the "short rains" from about mid-November to early January, and the "long rains" from March to May or June. Above about 1900 m. (6270 ft.), however, mists are frequent up to mid-September.

At Magamba near the lower and eastern edge of the reserve the rainfall averages a little over 50 in. (125 cm.) a year. At Sungwi near the western edge of the camphor forest the annual rainfall is about 57 in. (142 cm.) (Moreau, 1935, p. 11). Over the intervening country the average annual rainfall probably varies from 50 to 65 in. (125–162 cm.), or perhaps more, according to the aspect, the precipitation being higher on the slopes exposed to the south-east. In the Transvaal "mist belt forest" the rainfall is 70–80 in. (175–200 cm.) (Burtt Davy, 1926), and at Mufindi (1880 m.—6200 ft.) in the southern highlands of Tanganyika it is nearly 100 in. (250 cm.). Warm temperate rain forest is found in both these places.

On account of the favourable topographic and climatic conditions it is not necessary to protect any of the Usambara forests from fire. Mr W. F. Baldock, Senior Assistant Conservator of Forests, who knows the district well, states however that according to some of the oldest local natives the north-east

portion of the Magamba forest was destroyed by fire two or three generations ago. The forest in this area is certainly poorer than the average, is very varied in composition, and presented considerable difficulty when mapping the main communities. Apart from this corner and the few areas which have been cleared in the past by native cultivators (see p. 60), the forest may be considered as unaffected by fire.

GEOLOGY AND SOILS

Geology. Little detailed work seems to have been done on the geology of the Usambaras. They form part of the ancient (eozoic) crystalline complex of East Africa, consisting essentially of huge upthrust blocks of gneiss (Moreau, 1935). Some geologists (Gregory, Bauman and Jaeger), however, consider the south-west escarpment to be the north-east wall of a rift valley in which flows the Pangani river (Gregory, 1921, p. 288). The crystalline rocks range from acidic to intermediate, or even basic (Milne, 1935). Gregory (1921, p. 276) states that the strike of the eozoic rocks in the Usambaras trends from north-west to south-east. This explains the direction of the ridges which are the main topographic features of the Magamba forest. The dip, of course, is to the north-east.

Soils. The soils are mainly grey-brown, yellow-brown or dark brown "loams", or sometimes "sandy loams"; they become redder or pinker at a depth of 2–4 ft. (60–120 cm.) in the subsoil. They normally "have a considerable accumulation of dark-coloured acid humus in the top soil and a slightly bleached horizon below it" (Milne, 1936, p. 29).

Three profiles from soils bearing different forest communities were sampled by the writer early in 1935, and a profile under one of these communities was also sampled by Milne a few years earlier. Two of the writer's profiles, one from under a community (alt. 2070 m.—6830 ft.) with a ground flora of *Impatiens*, and one from under a community (alt. 2000 m.—6600 ft.) characterized by the complete absence of any ground flora, have proved to be "related to the podsols of northern European latitudes", and are referred to by Milne (1935) as "tropical forest podsols". Milne's profile, also sampled at 2000 m. and apparently under the same community ("no ground flora") as sampled by the writer at this altitude, is "a soil which, in spite of a great accumulation of humus at the surface, resembles a European 'brown forest soil' rather than a podsol, though it undoubtedly is on the border line between them" (Milne, 1935). This difference is believed to be due to a difference in the parent material, the "acidic" gneiss developing into a podsol and the "intermediate" or "basic" gneiss into a brown forest soil. It is difficult to understand why the vegetation should be apparently similar on these two different soils.

The writer's third profile, sampled under a community of "secondary" forest growth at 1700 m. (5600 ft.) "represents a type still further away from

a true podsol. At this lower altitude the red iron oxide colour is more strongly developed, and we have a fairly typical 'laterized red-earth'—with, however, the surface humus accumulation which links it with the podsolic or brown earth types" (Milne, 1935). Detailed analyses of the writer's three profiles, carried out by Mr W. E. Carlton, Assistant Soil Chemist at Amani, are given in Appendix I.

Warm temperate rain forest

Synonymy

Hohenwälder	Engler (1910)
Temperate rain forest	Troup (1922); Shantz & Marbut (1923)
High forest, Cloud forest	Under "temperate rain forest" in Shantz & Marbut (1923)
Mist belt forest	Burtt Davy (1926)
Mountain rain forest	Tansley & Chipp (1926); Rea (1935)
Mountain forest	Chipp in Tansley & Chipp (1926); Henkel (1930–1)
Subtropical evergreen forest	Phillips (1930); Snowden (1933)
Upper tropical evergreen or "rain" forest[1] ...	Phillips (1931 *a*)
Subtropical evergreen or "temperate rain" forest[1]	Phillips (1931 *a*)
High mountain temperate rain forest	Burtt Davy (1931)
Montane rain forest	Burtt Davy (1935)
Highland evergreen forest (community)... ...	Moreau (1935)

All these terms have been used to describe this one type of forest. The more applicable are "subtropical evergreen forest", "mountain rain forest", and "temperate rain forest". The term *subtropical* implies rather warm conditions such as are found on the central African plateau with its characteristic savannah types of vegetation; at Magamba, fires are necessary most of the year and the climate could hardly be called subtropical. *Mountain* is also a slightly misleading term, for the forests around Amani (about 1000 m. —3300 ft.) in the Eastern Usambaras are definitely "mountain" rain forests, but they are also decidedly tropical in nature (Moreau, 1933); at Knysna in South Africa, a type of forest similar to that at Magamba is found almost at sea level (Phillips, 1928; 1931 *c*). *Temperate* is not altogether a suitable term, for the climate is not strictly comparable with that of the north or south temperate zones, frost being very rare and snow quite unknown.

To describe this type of forest satisfactorily it seems therefore that a term is required which leaves out all question of altitude, for an increase here can be compensated by a decrease in latitude, the rainfall being about the same; a term is also required which implies something cooler than "subtropical" but warmer than "temperate". Dr Burtt Davy proposes to use the term "warm temperate rain forest", and the writer considers this to be the most satisfactory yet suggested.

[1] In Tanganyika, Phillips (1931 *a*) differentiates these two types on a basis of altitude—6000–6500 ft. The Magamba forest (5300–7600 ft.) includes many species from both of these types but it cannot be divided into them on such a basis.

General

The warm temperate rain forest at Magamba is a broad-leaved evergreen forest, even the conifers—*Podocarpus* spp.—having relatively broad leaves. The canopy is fairly dense and gives constant shade but it is not as dense as in tropical rain forest. There are usually four well-marked storeys or layers which may be referred to as the "dominant" storey, the "second" storey, the "undergrowth" and the "ground flora"; the dominant storey (70–120 ft. high) can usually be subdivided into an upper layer consisting of the dominant and co-dominant species, and a lower one consisting of the subdominants (see p. 61). Epiphytes are fairly common, especially on and near the edge of the escarpment. Lianes and creepers are common only in areas of secondary growth where man has interfered with the forest. The undergrowth or shrub layer generally is fairly thick, but the ground flora varies considerably in the different communities, being absent in one of the most extensive.

The Magamba forest is closely related floristically to the "temperate rain forests" of Kenya at altitudes of 7000–9000 ft. (2100–2700 m.) and with a rainfall of 55–60 in. (1400–1524 mm.) (Troup, 1922). It is also fairly closely related to the "high montane temperate rain forests" of Nyasaland at altitudes of 4000–7000 ft. (1200–2100 m.) (Burtt Davy, 1931), and to the "mountain forests" of Southern Rhodesia—altitude about 5000 ft. (1520 m.) and rainfall about 50–60 in. (Rendle *et al.* 1911; Henkel, 1930–1). There is also a generic relationship between it and the "mist belt" forests of the Transvaal (Burtt Davy, 1926), and the "moist" and "medium moist" types of the "subtropical evergreen forests" at Knysna, South Africa (Phillips, 1928; 1931*c*). All these forests could be described as *warm temperate rain forest.*

Other forests in West Usambara which are similar to the Magamba forest may be found in the forest reserves of Shagai, Baga, Ndelemai and probably Mkusu (higher parts). It is not known, however, to what extent the communities described below are developed in these forests, except that "heathland" is common to all. On Kilimanjaro (but not on the northern slopes) there is a zone of "camphor" forest; somewhat similar forests, but without *Ocotea*, also occur on Mt Meru and on the Mbulu highlands. On the Ufiume-Mikiulu uplands and Mts Ufiume and Hanang in the Northern Province of Tanganyika the subtropical evergreen forest of Phillips (1930) differs mainly in the absence of *Ocotea*. On the Nguru and Uluguru mountains the forests appear to be of a less temperate nature (Moreau, 1933; Rea, 1935), but little has been published about them. There are some very fine stands of *Piptadenia buchananii* Bak. in the Derema reserve in the North Ngurus; this species is not found in the more temperate forest regions, such as Magamba. Would not the term "subtropical evergreen forest" be more suitably confined to describing such forests as these?

Not much has been published about the detailed composition of the forests

along the Kiberege-Dabaga-Mufindi escarpment in the Southern Highlands Province (rainfall 80–100 in. (2030–2540 mm.)) or of those on the Porotos and Livingstone mountains north of Lake Nyasa (rainfall probably over 100 in.). From the writer's own observations and those of other forest officers, it seems that the Dabaga and Mufindi forests were originally very similar to the Magamba forest; to-day, they are nearly all secondary, having been cleared in the past by native cultivators. The Livingstones and Porotos are regions of recent volcanic activity and their forests are somewhat different (the dominants are *Entandophragma* and *Chrysophyllum* or else *Bambusa arudinaria* var. *alpina*); comparisons based on only brief observations are therefore rather difficult, especially as these forests too have suffered at the hands of native cultivators.

In the Magamba forest, with the exception of small areas of heath, of swamp, and of poor open secondary forest, the dominant trees are camphor (*Ocotea usambarensis*) and *Podocarpus* spp.; *P. usambarensis* occurs mainly in the drier northern portion, and *P. milanjianus* (or *P. mannii* or *P. falcata*) over most of the forest, except in the southern part, which however it is slowly invading. The co-dominant species (in a silvicultural, not in a numerical sense), the shrubs and the ground flora, but not so much the subdominant and second storey trees, vary considerably in the different communities which are to be found in the forest. Actually, in the course of the field work some twenty-six communities were recognized; these are of very varying ecological rank and differ much in area; many of the less important ones have not been sufficiently studied, and as several of them are probably only local variations of the important communities, they will not be described separately in this paper.

Primary succession

The primary successional changes observed in the course of the enumeration included the following:

a *hydrosere* starting from swamps, and

a *xerosere* starting from heathland (the earlier stage—a *lithosere*—from bare rock to heath has already been completed).

(*a*) *The hydrosere.* The sere starts on the narrow (5–50 yd.) alluvial plains found only in the vicinity of the Magamba forest station. The vegetation of these swampy areas consists mainly of the fern *Dryopteris gongylodes*, together with some grasses, reeds (*Typha* and *Pennisetum*) and a mauve-flowered composite with spiny leaves. As the level of the ground rises by the accumulation of silt, shrubs such as *Hypericum lanceolatum* come in, followed by small trees such as *Myrica kilimandscharica* and *Agauria salicifolia* (Ericaceae) and a thick layer of litter and humus is built up. *Aphloia myrtiflora* (Flacourtiaceae), *Xymalos monospora* (Monimiaceae) and two species of *Lasianthus* (Rubiaceae) then appear, followed by *Ocotea usambarensis* (Lauraceae)—

probably as root suckers from trees on adjoining higher ground—*Podocarpus milanjianus*, *Pygeum africanum* (Rosaceae) and *Rapanea usambarensis* (Myrsinaceae). No further stage was observed, except that in front of the Magamba house many of the camphor trees have become stag-headed or have died, and have been exploited for their timber. Interference by man in the past, and present clearing for cultivation has made it impossible to investigate fully this dying off; perhaps it is due to a change in the level of the water table.

(*b*) *The xerosere.* This sere starts between "boulders" which are mainly siliceous rather than lateritic in composition: their origin is unknown. Growing between the boulders in the numerous pockets of dark brown sandy loam is the characteristic tree heath—*Philippia holstii* (Ericaceae)—together with the shrub *Dodonaea viscosa* (Sapindaceae), which has red-winged fruits. Associated with these are two small papilionaceous shrubs, one with mauve flowers, and the other—*Smithia mildbraedii*—with yellow flowers and a sticky inflorescence. There are also the bracken fern—*Pteridium aquilinum*—*Lycopodium* sp., a small pink-flowered orchid and a small mauve lobelia.

As further pedogenic processes take place small trees of *Myrica kilimandscharica*, *Agauria salicifolia*, and *Aphloia myrtiflora*, and shrubs such as *Rhamnus prinoides* at low altitudes, or *Memecylon* sp. (Melastomaceae) at over about 2000 m., appear, replacing the bracken, herbs and papilionaceous shrubs, though the heath and *Dodonaea* still persist.

In the next stage of the sere, a stage always found surrounding the above community, the heath, *Dodonaea* and *Rhamnus* have disappeared, and *Agauria* is found only as old trees—an indication that the earlier community once existed. In their place young trees of the main forest species are found, e.g. *Ocotea*, *Rapanea usambarensis*, *Syzygium cordatum* (Myrtaceae), together with smaller trees such as *Trichocladus malosanus* (Hamamelidaceae), and *Olea hochstetteri*. A definite shrub layer also develops composed of *Memecylon* sp., *Lasianthus* sp.nov. and *Grumilea buchananii* (Rubiaceae): a small mauve-flowered balsam, *Impatiens pseudoviola* (Balsaminaceae), is often found on the forest floor.

This stage gives way to what is probably a climax community of high forest, and one which is rather similar to that developed from the hydrosere. In this community *Agauria* and *Myrica* have disappeared. The dominant tree is *Ocotea*; it is associated with some *Rapanea*, *Podocarpus milanjianus*—absent in the southern corner—and a few *Teclea nobilis* (Rutaceae). There is a fairly definite second storey of *Syzygium*, *Macaranga kilimandscharica* (Euphorbiaceae), *Trichocladus* and *Aphloia*. The undergrowth is composed of a fairly thick layer of small shrubs of *Lasianthus* sp.nov., *L. kilimandscharicus* (rare above 2000 m.), *Grumilea* and *Memecylon*. There is no ground flora—a characteristic feature of this community.

Secondary succession

There are two causes of secondary succession at Magamba—landslides (*edaphic*), and native cultivation (*biotic*).

(*a*) *The edaphic subsere.* This is only found in a few small patches scattered over the forest. It was not possible to work out the full succession, though the early stages are clearly recognizable. The bare ground after a landslide (these are not frequent) is first covered with a moss, and then a fairly dense growth is developed of the tree lobelia. This gives way to a thicket of shrubs composed of *Solanum schumannianum*, *Grumilea platyphylla* (Rubiaceae), *Pavetta dalei* (Rubiaceae), *Piper capensis*—above about 2000 m.—and "Ngulanguzwa", a shrub with long broad leaves having persistant leafy stipules. Creepers and lianes help to make these thickets impassable except along cut paths. A probable later stage consists of open forest of *Albizzia gummifera* (Mimosaceae), *Macaranga*, *Catha edulis* (Celastraceae), and *Cussonia spicata* (Araliaceae) over a less dense form of the above thicket.

(*b*) *The biotic subsere.* About 10% of the forest consists of secondary growth on land once (or sometimes twice) burnt and cleared for native cultivation. Although no known records exist, it is fairly evident that the natives were evicted from these areas in German times when the forest was demarcated as a reserve. These areas of secondary growth are found at or fairly near the edges of the reserve, mainly on the eastern (Magamba) side, though some strips stretch for over a mile into the forest up one or two valleys. The fact that more or less the same stage (community) in the sere is to be found in most of these areas rather suggests that they were all left at about the same time.

Unless grazed and browsed over, when grassland will develop, deserted fields are usually quickly colonized by a thick mass of herbs, of which a mauve-flowered composite, *Erlangea* sp., is about the commonest. Various shrubs, including *Solanum*, *Dodonaea* (sometimes in almost pure stands), *Cluytia mollis* (Euphorbiaceae), *Grumilea platyphylla*, and *Pavetta dalei* come in together with a few giant lobelias, "Ngulanguzwa", and a fairly dense herbaceous growth of an acanthaceous plant, "Mshikise". Various trees forming a very open upper storey then appear, e.g. *Cussonia*, *Maesa lanceolata* (Myrsinaceae), *Allophylus abyssinicus* (Sapindaceae), *Albizzia*, *Macaranga*, *Catha* (sometimes), *Polyscias kikuyuensis* (Araliaceae) and *Dombeya leucoderma* (Sterculiaceae); there is still a dense undergrowth of shrubs matted together with lianes and creepers. Some trees of *Pygeum africanum* (Rosaceae) and the deciduous *Clausena melioides* (Rutaceae) are usually found in these areas of secondary forest. They may have been left when the original forest was cleared, but it is believed that the cultivation of the soil following clearing may have some favourable effect on their development; the average volume per acre of *Pygeum*, though low, is higher in this community than it is in

nearly all the others, and *Clausena* is rarely found in this forest in any other community. On the northern slopes of Kilimanjaro, however, *Clausena* occurs fairly frequently in the "middle" or "pillarwood" (*Cassipourea elliottii*) zone, a zone which has been quite undisturbed by man.

The stages in the sere naturally vary somewhat in different localities, mainly on account of soil differences; and, although this fact was appreciated during the field work, it was not possible to investigate the variations more fully.

A minor community—*medium secondary forest*—forming closed canopy forest but with no trees of timber size, possibly a variation in the biotic subsere, is composed of *Aphloia*, *Myrica*, *Rapanea*, *Albizzia*, *Cussonia* and *Xymalos*, with an undergrowth of *Rhamnus* and *Grumilea platyphylla*, and a ground flora of grasses and seedlings of *Grumilea*. This community possibly develops as the result of interference by man with some intermediate stage of the xerosere.

Another community with a closed canopy—*good secondary forest*—which is probably one of the later subseral stages is sometimes met with composed of *Ochna holstii*, *Catha*, *Teclea grandifolia*?, *Macaranga*, *Bersama volkensii* (Myrsinaceae), *Allophylus*, *Pygeum*, *Lachnopylis* (Loganiaceae), *Albizzia*, *Aphloia* and *Cussonia*. There is a tall shrub layer of *Halleria lucida* (Scrophulariaceae), *Grumilea platyphylla*, *Psychotria alsophila* (Rubiaceae) and sometimes the large-leaved *Dracaena papahu* (Liliaceae). The ground flora is poorly developed, consisting usually of a little grass with "Mshikise" (Acanthaceae) in the more open places.

Description of important communities of the forest

Throughout this paper all specific names are written with small initial letters, in keeping with the practice of the Imperial Forestry Institute, Oxford.

In the following descriptions the term "co-dominant" refers to trees in the upper canopy whose frequency is less than that of the dominants. "Subdominant" refers to slightly smaller trees which are growing *between* rather than *underneath* the dominants and co-dominants; their frequencies may be higher or lower than those of the latter. Trees which normally have their crowns beneath those of the dominants and co-dominants are referred to as "second storey" trees.

A full list of the species occurring in each community, and their frequencies, are given in Appendix II, together with the author's and the native (Kisamba) names. An alphabetical list of native names with the botanical equivalents is given in Appendix III.

The following frequency scale has been adopted: 5 = very abundant, 4 = abundant, 3 = frequent, 2 = occasional, 1 = rare. Frequency numbers in brackets in Appendix II indicate a low constancy; by this is meant that the plants were recorded in less than half the number of samples in the community.

The following approximate divisions of altitude have been used:

Low	1600–1850 m.	(5280–6100 ft.)
Lower	1600–1950 m.	(5280–6430 ft.)
Medium	1850–2050 m.	(6100–6700 ft.)
Upper	1950–2300 m.	(6430–7590 ft.)
High	2050–2300 m.	(6700–7590 ft.)

(i) Ocotea-Podocarpus-Lasianthus *spp.: no ground flora.* This community, the largest and the most widely distributed, with its seral stages from heathland, covers 3800 acres (approx.) or 23% of the total area of the forest. In altitude it occurs from 1650 to 2275 m. (5450–7500 ft.). It is usually found on the tops of ridges and along the "dip" (north-east) slopes where the drainage is good; it appears to be confined to relatively dry soils. The soil is generally a fine dark brown loam, podsolitic, and remarkably acid, sample profiles showing *p*H values of 3·0 and 3·4 at 1–6 and 6–10 in. respectively. (See Appendix I, samples Nos. 2586–2594 for analytical data.)

The main features of this community are the absence of any ground flora, and the fact that its invasion by *Podocarpus milanjianus* is not yet complete. At lower altitudes (in the southern corner) there is hardly any *Podocarpus*, but this corner is definitely being invaded from the higher regions; as the altitude increases more and more seedlings appear, then poles, then young trees and finally all these together with the older seed trees. Near the Magamba house (1700 m.) there is a small area of this community with a dense undergrowth of *Podocarpus* poles; possibly these are from seed sown in German times.

The undergrowth is composed mainly of one or both species of *Lasianthus* (Rubiaceae); *L. kilimandscharicus* is usually found in the lower portion of any area of the community, though rarely above altitudes of 2000 m. and *Lasianthus* sp.nov. usually in the upper portion. Both species generally occur in the middle portion, unless it is too high for the former one.

The dominants are *Ocotea usambarensis*—a fine-looking dark-foliaged tree with a red-brown bark, and *Podocarpus milanjianus*—small (less than 1 in. long) fruits on a fleshy receptacle. The average height of these trees is about 80 ft. (24 m.). The common co-dominants are *Rapanea usambarensis* (Myrsinaceae)—a tall tree with a good straight bole and rhododendron-like leaves, *Ficalhoa laurifolia* (Ericaceae)—a tree with a fairly straight bole, a red-brown bark with characteristic excentric markings and a yellow latex, and *Teclea nobilis*—a tall well-shaped tree with trifoliate leaves. Less frequent are *Pygeum africanum*—with a characteristic bark of hard grey-black scales, *Ilex mitis*—usually riparian and poorly shaped, and *Ochna holstii*—a fairly straight bole, and with yellow flowers (this tree is found only at lower altitudes). Other co-dominants are *Cassipourea elliottii* (Rhizophoraceae)—wood very hard, *Craibia elliottii* (Papilionaceae, syn. *Schefflerodendron* sp.), *Croton* sp. nr. *C. scheffleri* (Euphorbiaceae), *Faurea* sp. (Proteaceae), *Lachnopylis* sp.

(Loganiaceae)—a much fluted trunk, *Podocarpus gracilior*, *Strombosia* sp. (Olacaceae), *Casearia* sp. nr. *C. engleri* (Flacourtiaceae) and *Apodytes dimidiata*? (Icacinaceae)—the last two being both tall, well-shaped trees.

The common subdominants are *Macaranga kilimandscharica* and *Syzygium cordatum* (Myrtaceae) with cream-coloured bark and excentric markings. Others are *Adinandra schliebenii* (Theaceae)—at higher altitudes only, and *Bersama volkensii* (Myrsinaceae).

The second storey is usually composed of *Olea hochstetteri*—generally on or near ridges, *Tricholadus malosanus* (Hamamelidaceae) with white indumentum on the under surface of its leaves, *Aphloia myrtiflora* (Flacourtiaceae syn. *Neumannia theaformis*), *Teclea grandifolia*?—leaflets about twice as long as those of *T. nobilis*, a variety of *Gymnosporia lepidota* (Celastraceae), and "Mfumbati No. 2" (Araliaceae). Young trees of the dominants, co-dominants and subdominants of course are also present.

In the undergrowth, besides the two species of *Lasianthus*, there are *Urophyllum holstii*, *Grumilea buchananii*, *Psychotria alsophila*, and *Psychotria* sp. (No. 404)—all Rubiaceae, and also, at higher altitudes, *Memecylon* sp.—a small (4–8 ft.) shrub with small round opposite leaves. Occasionally there are some *Gymnosporia* sp. (Celastraceae) and *Clausena anisata* (Rutaceae).

There is no herbaceous ground flora, but the soil is covered with a thick layer (about 6 in.) of organic matter. Regeneration of camphor by root suckers is abundant, though very few ever get as far as the pole stage; seedlings of *Podocarpus* are fairly common even at low altitudes where there are very few large trees—the seeds probably being distributed by birds, e.g. the wood-pigeon (*Columba arquatrix*).

The seral stages from heathland to this community have been referred to and have been briefly described above (p. 59).

At high altitudes on and near the tops of ridges this community is sometimes rather open and the trees stunted; there are some ramblers (No. 408) and *Rubus* sp. present in the undergrowth, and some scattered Acanthaceae form a ground flora. Such areas however are small and unimportant. Sometimes where the ground is almost level a low (2–4 ft.) dense layer of the small shrub *Psychotria alsophila* is developed. The other shrubs and trees are typical of the main community. These areas are also very small and of no practical importance.

(ii) Ocotea-Podocarpus-Ficalhoa: *ground flora of large balsam*. Both in respect of soil moisture and of atmospheric humidity, this community is confined to the wetter parts of the forest, and it is therefore found only in the south-western portion, i.e. at and near the edge of the escarpment. It is best developed on the shelf below the north-west portion of the Irente-Sungwi ridge. It covers an area of about 2500 acres or 15% of the forest, and in altitude it varies from 1800 to 2200 m. (6000–7250 ft.). The soil is generally a very dark brown or a black sandy loam; it is also podsolitic and very acid,

sample profiles showing pH values of 3·15 and 3·25 at 1–5 and 5–9 in. respectively. (See Appendix I, samples Nos. 2579–2584 for analytical data.)

The most characteristic features are the presence of a greater or lesser number of tree ferns—*Cyathea* sp.—and a ground flora composed generally of a dense stand of *Impatiens splendens*?, a large (2–5 ft.) balsam with large pale mauve flowers. In hollows and along stream banks where the soil may be more or less waterlogged almost pure stands of tree ferns occur, with some balsam and a few ordinary ferns forming a ground flora. The height of the tree ferns varies from about 15 to 30 ft.

On ridges where the soil is much better drained this community tends to resemble the previous one ("no ground flora"), but it may be distinguished from it by the presence of the ground flora and the higher proportion in the undergrowth of *Grumilea buchananii* to the two species of *Lasianthus*.

The dominants are *Ocotea* and *Podocarpus milanjianus*, with *Ficalhoa* as the commonest co-dominant. In height they average about 90 ft. The commoner co-dominants, besides *Ficalhoa* are *Adinandra schliebenii* (Theaceae) (stem often rotten and hollow, corolla red, about 2 in. long and ½ in. wide), *Chrysophyllum albidum* (Sapotaceae) (a tall tree up to 120 ft. in height, with a much buttressed stem, a milky latex and a whitish indumentum on the underside of the leaves), *Pygeum*, *Rapanea*, and *Teclea nobilis*. Less frequent are *Ilex*, *Strombosia*, *Faurea*, *Ochrocarpus africanus* (Guttiferae) (with a yellow sticky latex and large simple opposite coriaceous leaves), *Casearia* and *Apodytes*. The subdominants are *Macaranga* and *Syzygium*.

Trees in the second storey are *Dasylepis leptophylla* (Flacourtiaceae), *Trichocladus*, "Mfumbati No. 1", *Canthium* sp. (Loganiaceae), and *Gymnosporia lepidota*.

Besides the tree fern, *Cyathea usambarensis*?, *Grumilea* and *Lasianthus* spp., the undergrowth generally consists of *Psychotria* sp. (No. 404), *Memecylon* and *Moustea grandiflora* (Scrophulariaceae) (with white flowers). The ground flora consists almost entirely of balsam, with a few suckers of camphor and seedlings of *Podocarpus* and *Ficalhoa*; occasionally a few Acanthaceae are present.

(iii) Podocarpus-Ocotea: *dense ground flora of Acanthaceae and small balsam*. Like the "no ground flora" community, this one is found on well-drained soils, but (unlike it) has a dense low (about 2 ft.) ground flora of an acanthaceous herb and a small pale mauve-flowered balsam: also, it does not occur much below 2000 m. The canopy is more open than in either of the preceding communities and the trees are often decked with lichens; they are smaller and not so well shaped, and the stocking is lower than in most of the other communities. The average height is about 60 ft. (18 m.). The area covered is about 2350 acres or 14% of the forest. Altitude, 1975–2300 m. (6500–7600 ft.). The soil is a brown loam, generally with some bleached quartz grains. It is probably also podsolitic but it was not possible to collect sample profiles.

The dominants are the same as before, though here *Podocarpus* is about twice as frequent as *Ocotea*. The main co-dominants differ little from those of the preceding communities; *Ficalhoa* is confined to the south-west half of the forest (higher atmospheric humidity); fairly common are *Pygeum* and *Rapanea*, and less frequent are *Adinandra*, *Ilex* and *Cornus volkensii* (generally riparian). *Strombosia*, *Apodytes* and *Casearia* were not recorded. *Macaranga* and *Syzygium* are here co-dominant rather than subdominant. *Trichocladus* is a subdominant, and "Mfumbati No. 2", *Dasylepis*, *Teclea grandifolia*?, and *Gymnosporia* are present in the second storey.

The undergrowth consists mainly of *Lasianthus* sp.nov., and *Grumilea buchananii*, with some *Memecylon*, *Lasianthus kilimandscharicus*, *Psychotria* (No. 404), *Pavetta dalei* (Rubiaceae), and some tree ferns.

In the ground flora, besides the Acanthaceae[1] and small balsam (*Impatiens pseudoviola*), there is frequently the small *Pilea engleri* (Urticaceae), and sometimes a pale purple-flowered scrophulariaceous herb (*Salvia*?) which occurs mainly on south-west aspects (moister) and where the tree ferns are more numerous. Regeneration of *Ocotea* and *Podocarpus* is poor.

(iv) Ocotea *and others: varied ground flora.* The main difference between this and the "no ground flora" community is the presence here of a varied ground flora of grass, or small scattered herbs, or fairly dense patches of acanthaceous subshrubs. The stocking is lower than it is in most communities, being very little higher than in the preceding one. The altitude varies from 1615 to about 2000 m. (5300–6600 ft.). The area covered is about 12% of the forest (2000 acres).

It occurs mainly between the "no ground flora" community and the areas of secondary forest or the open areas around the villages of the forest squatters. To some extent it has been interfered with by man, as the smaller size classes (poles) are often abnormally low. It is this removal of the smaller trees for building poles which probably has increased the light intensity in the lower layers of the forest and permitted the development of a ground flora; the variations in this flora are probably due partly to the degree to which the light intensity has been increased and partly to minor soil differences. The number and variety of the co-dominant species suggests, however, that more complex factors than the mere cutting out of poles have been at work. The soil is brown and varies from a sandy loam to a loamy sand, though sometimes it is redder and somewhat clayey.

Ocotea is the only true dominant—average height about 75 ft. (23 m.), *Podocarpus* spp. (*P. milanjianus*, *P. usambarensis* and *P. gracilior*—rare) being usually of occasional occurrence only. The co-dominants, which vary somewhat from place to place, are *Catha edulis* (Celastraceae), *Ochna*, *Rapanea*, *Teclea*

[1] Although several different species of the Acanthaceae were observed in the field, and were used in helping to recognize this and other communities, only two were found in flower, and it has proved impossible to name the others from their leaves only.

nobilis, *Chrysophyllum*, *Cassipourea*, *Croton*, *Bersama*, *Ekebergia rueppeliana* (Meliaceae), *Ilex*, *Lachnopylis* and *Albizzia gummifera* (Mimosaceae). At the lower limits of this community a few trees of *Mitragyna rubrostipulata* (Rubiaceae), *Mimusops* sp. (Sapotaceae) and *Parinarium holstii* (Rosaceae) were observed; these are all more frequent in nearby forests at altitudes below 1600 m. (5280 ft.).

The subdominants too vary a little; they are *Macaranga*, *Allophylus abyssinicus*, *Syzygium*, *Conopharyngia* sp. (Apocynaceae)—a light brown corky bark and a milky latex, and *Myrica*.

Trees which form the secondary storey are *Dasylepis*, *Teclea grandiflora*?, *Aphloia*, *Olea*, *Cussonia spicata* (Araliaceae), *Xymalos monospora* (Monimiaceae), *Gymnosporia*, "Kireiti", and rarely *Peddiea fischeri*, *P. volkensii* (Thymelaeaceae), *Sclopia* sp. (Flacourtiaceae), *Ixora albersii* (Rubiaceae) and *Oxyanthus speciosus* (Rubiaceae).

The undergrowth also varies in density and composition. Usually present are *Pavetta dalei*, *Grumilea platyphylla* (taller and with larger leaves than *G. buchananii*), *Rhamnus prinoides*, *Dracaena papahu*, *Halleria lucida* (Scrophulariaceae), *Lasianthus kilimandscharicus*, and rarely *Moustea* and *Maba natalensis* (Ebenaceae). Lianes and creepers generally occur but are not abundant. Sometimes there are only *Pavetta*, *Dracaena* and a dense low (2–3 ft.) growth of *Chasalia*. The ground flora has been referred to above. Occasionally a thick carpet of *Selaginella* sp. is encountered. Regeneration of camphor (*Ocotea*) and *Podocarpus* is rather poor.

(v) Podocarpus-Ocotea-Chrysophyllum: *ground flora of* Isoglossa lactea. In the valleys away from the escarpment and at medium altitudes (1750–2050 m., 5780–6700 ft.) a community is developed which is probably the most densely stocked in the forest. Although *Podocarpus* and *Ocotea* are only about as frequent as in the community with a ground flora of Acanthaceae and small balsam, many more stems are present proportionally of the co-dominant species. The area covered is about 1800 acres (11 %). The soil is a dark brown sandy loam with a lighter brown or yellower, somewhat clayey, subsoil. The dominants are *Podocarpus* species, mainly *P. milanjianus*, and *Ocotea*. The average height is nearly 100 ft. (30 m.).

The commonest co-dominant, and one rather characteristic of the community, is the large *Chrysophyllum*, which here often reaches heights of 100–120 ft. (30–36 m.). Other common co-dominants are *Ficalhoa* (not found in the north-east part), *Teclea nobilis*, and *Cassipourea*. Less common are *Entandophragma* sp. (a large slightly buttressed tree up to 140 ft.), *Rapanea*, *Cornus*, *Pygeum*, *Polyscias kikuyuensis* (Araliaceae) (in open patches), *Strombosia*, *Podocarpus gracilior* and *P. usambarensis*.

The common subdominants as usual are *Macaranga* and *Syzygium*; also present are *Craibia*, *Ochna* and *Conopharyngia*. The second storey is composed of *Aphloia*, *Dasylepis*, *Teclea grandifolia*?, *Trichocladus*, *Gymnosporia* and "Mfumbati No. 2".

The main shrub in the undergrowth is *Lasianthus kilimandscharicus*; others present are *Pavetta*, *Lasianthus* sp.nov., *Grumilea platyphylla* and *Urophyllum*. Tree ferns may also be present.

Dominant and characteristic among the acanthaceous ground flora is a small subshrub (2–4 ft.) with white flowers having purple markings on the corolla—*Isoglossa lactea*. *Crossandra tridentata* (Acanthaceae) is also often present, occasionally to the exclusion of all other herbs. At least two other members of the Acanthaceae are generally present in small numbers. Regeneration of *Podocarpus* and *Ocotea* is rather poor.

(vi) *Poor open secondary forest.* This community, which has developed on deserted cultivated or only cleared land, has been referred to above in describing the biotic subsere. The area covered by it is about 1700 acres (10%). It is not found above 1900 m. (6270 ft.). The soil is mostly a brown to reddish brown coarse loam, though sometimes it is clayey with coarse rock particles. A sample profile taken at Magamba proved to be a "laterized red earth". (See samples Nos. 2596–2601 in Appendix I.)

As the trees do not form a closed canopy they cannot be said to be either dominant or subdominant as regards height. Those usually present are *Albizzia*, *Allophylus*, *Catha*, *Macaranga*, *Polyscias*, *Pygeum*, *Dombeya leucoderma* (pink flowers), *Cussonia* and *Maesa lanceolata* (Myrsinaceae); less frequent are *Clausena melliodes* (Rutaceae) (a tall (70 ft.) deciduous tree with characteristic lenticels), *Croton*, *Euclea* sp. (Ebenaceae) *Ritchiea albersii* (Capparidaceae), *Trema guineensis* (Ulmaceae) and *Vangueria edulis* (Rubiaceae).

The common shrubs forming a thicket undergrowth are *Pavetta*, *Solanum schumannianum* and *Grumilea platyphylla*. Also present are *Dodonaea viscosa*, *Cluytia mollis* (Euphorbiaceae), *Dracaena*, "Ngulanguzwa" and the giant lobelia. Brambles, creepers and lianes are abundant. A ground flora of acanthaceous subshrubs is generally present.

(vii) *Open forest at higher altitudes.* On the steep ("strike") slopes below Sungwi peak, and in some other parts of the forest on the strike faces of the ridges at altitudes from about 1900 to 2250 m. (6270–7420 ft.), rather open forest is encountered. The soil is shallow and is a brown coarse or heavy sandy loam; boulders are generally present. The area covered by this community is only about 600 acres (3·6%). It varies somewhat in composition and a relatively large number of species are to be found in it. The average height of the taller trees varies from 60 to 80 ft. (18–24 m.).

The dominant species are *Podocarpus milanjianus*, *P. usambarensis* and *Ocotea*, the two Podocarps together being more than twice as frequent as the camphor.

The co-dominants are *Ficalhoa* (frequency only exceeded in the community with a ground flora of large balsam), *Pygeum* (more frequent here than anywhere else), *Entandophragma* (frequency only exceeded in the community

with a ground flora of *Isoglossa lactea*), *Chrysophyllum*, *Rapanea*, *Teclea nobilis* and *Ochrocarpus*. Less frequent are *Bersama*, *Adinandra*, *Cassipourea*, *Croton*, *Cornus*, *Ilex*, *Lachnopylis*, *Pittosporum abyssinicum*, *Strombosia* and *Casearia*. The subdominants are *Macaranga*, *Syzygium*, *Conopharyngia*, *Craibia* and *Dombeya* (indicating secondary growth).

In the secondary storey are *Olea*, *Dasylepis*, *Aphloia*, *Canthium*, *Gymnosporia* and "Mfumbati No. 2".

The undergrowth varies somewhat and so does the ground flora. *Lasianthus kilimandscharicus*, *Psychotria* sp. (No. 404) and *Pavetta* are nearly always present. In some places there are also *Grumilea buchananii*, *Piper capensis* and a ground flora of various herbs, mainly Acanthaceae; in other places the main shrubs are *Pavetta* and *Grumilea platyphylla*, with some *Lasianthus* and *Psychotria* and a ground flora of large balsam.

(viii) Ocotea: *ground flora of Acanthaceae.* This community, though covering only about 70 acres (0·4 %), is of interest and importance as it consists of forest with a very high stocking of camphor; some of the largest specimens of this tree are to be found here. The average height is about 90 ft. (27 m.). The community is confined to a narrow strip about 200 yd. wide along the middle part of the "strike" slope of one of the main ridges above Irente. The altitude varies from 1750 to 2050 m. (5780–6700 ft.). The soil is a deep brown loam. The slope has a southern aspect, but the local topography is such that it receives the full benefit of the moisture-bearing winds.

The only other trees which occur here are a few *Rapanea*, *Teclea nobilis*, *Bersama* and *Pittosporum*. The subdominants are *Macaranga*, *Syzygium* and *Conopharyngia*, and the second storey is composed of *Aphloia*, *Trichelia volkensii* (Meliaceae), *Teclea grandifolia*?, *Xymalos* and "Mfumbati No. 2".

The undergrowth, which is not at all dense, consists of both species of *Lasianthus*, *Urophyllum*, *Pavetta* and a few tree ferns. The ground flora is a tall dense growth (about 4 ft. high) of two species of Acanthaceae.

Important communities other than forest

There are two other communities which are of considerable ecological importance, though they only cover small areas and are of no economic value.

(ix) *Heath.* This community has been referred to and described above as being the "starting point" of the xerosere. It covers about 100 acres (0·7 %). The altitude varies from 1750 to 2050 m. (5780–6700 ft.), though heath trees are occasionally found on ridges as high as 2270 m. (7380 ft.).

(x) *Swamp.* This community has also been referred to and described above; it is the "starting point" of the hydrosere. It covers an area of about 60 acres (0·3 %), and the altitude varies from 1630 to 1670 m. (5390–5520 ft.). It occurs only in the vicinity of the Magamba Forest Station.

Minor communities

The following communities, which are probably of very varying ecological rank, do not cover large areas in the forest and therefore will not be described in any detail, though most of them have been referred to already in the section on Succession. Their total area is about 1500 acres (9%).

(*a*) *Heath and associate arborescent species.* Seral from heath; referred to under the xerosere (p. 59).

(*b*) *Arborescent associates of heath and* Lasianthus. Seral from above; referred to under the xerosere (p. 59).

(*c*) Ocotea-Podocarpus: Lasianthus *and ramblers.* Referred to as a variation, occurring on ridges, of the "no ground flora" community (p. 63).

(*d*) Psychotria alsophila. A society(?) occasionally found on badly drained soils in the "no ground flora" community.

(*e*) *Medium secondary forest.* Referred to in the section on the biotic subsere (p. 60).

(*f*) *Good secondary forest.* Also referred to in the section mentioned above.

(*g*) "*Cliff*" *forest.* An extreme form of the "open forest at higher altitudes"; found only on precipitous slopes.

(*h*) *Tree ferns.* A society often developed in the community with a ground flora of large balsam, and also sometimes in other communities on badly drained soils.

Possible ecological relationship of the important communities

The writer has not yet had sufficient experience in ecological work to feel justified in committing himself either to the "mono-climax" theory as advanced by Clements (1916), Phillips (1934–5) and others, or to the "poly-climax" theory of such workers as Bourne (1934) and Michelmore (1934). Nor does he consider it advisable at this stage definitely to rank the main communities which have been described above. Tentative suggestions as to their ecological rank and to their relationships are given below, but it must be emphasized that these are only provisional, and that further work must be done in the field before any definite conclusions can be drawn.

The community of Ocotea-Podocarpus-Lasianthus *with no ground flora* is probably an association, if the use of a climax rather than a seral term is permitted, in spite of the fact that colonization by one of its dominants is not yet complete. The seral stages leading up to it from heathland have been recognized and described; it also appears to develop from swampland. The rocks on which heath is found are by no means typical of the gneisses found under most of the forest, and it is doubtful if heath was ever the original vegetation on all the areas now under this community; it is probable that there is another xerosere starting on soils derived from gneiss, but that its seral stages are no longer present.

The community of Ocotea-Podocarpus-Ficalhoa *with ground flora of large balsam* is probably an association whose existence depends on a higher degree both of soil moisture and of atmospheric humidity than that necessary for the other communities. It occurs in localities where mists are prevalent for many months of the year. Its seral stages are unknown.

The community of Podocarpus-Ocotea *with dense ground flora of Acanthaceae and small balsam* is probably an association which has developed at the higher altitudes on relatively dry soils, possibly less fertile than those of the "no ground flora" community. Its seral stages are also unknown.

The community of Ocotea *and other species with varied ground flora* is perhaps an associes in a subsere resulting from only slight interference by man with the "no ground flora" community; this statement must be accepted with caution, however, for the number and variety of the co-dominant species suggests a more complicated origin. The *Ocotea* is often over-mature and suffers from a "heart-rot" fungus.

The community of Podocarpus-Ocotea-Chrysophyllum *with ground flora of* Isoglossa lactea is probably an association whose existence depends on a high degree of soil moisture, but is one which does not require such a high atmospheric humidity as the "large balsam ground flora" community. Its seral stages also are unknown.

The Poor Open Secondary Forest appears to be an associes in a biotic subsere. The original vegetation was probably either of the "no ground flora" type or of the "ground flora of *Isoglossa lactea*" type. It is not known if it will develop to normal forest again; the possibility of its colonization by camphor seems doubtful, as all the regeneration of this species seen elsewhere in the forest was by root suckers or coppice. It is more likely that it will develop into a characteristic subclimax community.

The Open Forest at higher altitudes is possibly an associes or a subclimax community in a xerosere (lithosere), its further development being rather hindered by the steep slopes, which prevent the normal processes of soil formation from taking place. It may represent a seral stage to some of the other communities.

The Ocotea *community with ground flora of Acanthaceae* is possibly a consociation related to the "no ground flora" community, the habitat factors being favourable to the development of camphor to the exclusion of the other dominants and to most of the usual co-dominants; the partial suppression of the second storey and of the undergrowth has probably resulted in an increase of the light intensity near the ground, and this has favoured the development of a ground flora.

The Heath and Swamp communities are probably both associes, the relationships of which have been dealt with above in the section on Primary Succession (p. 58).

The diagram (p. 71) indicates in schematic form the suggested relationship

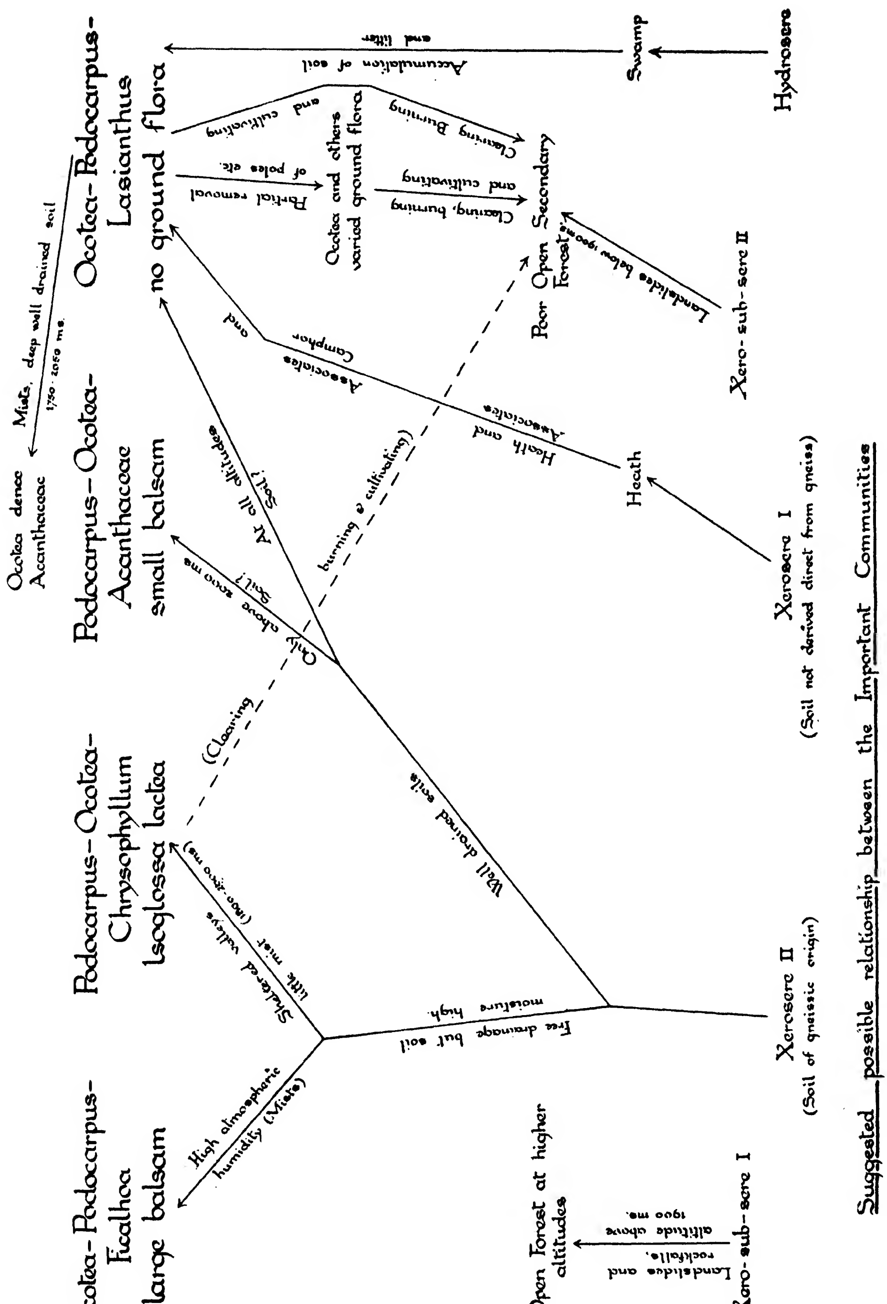

FIG. 2. Diagram showing the suggested possible ecological relationship between the important communities.

between the communities. The altitudinal divisions are, of course, only approximate.

Forest types

Foresters are appreciating more and more the value of the recognition of "forest types" as an aid to the efficient management of their forests, both from the point of view of assessing the quality of the locality for purposes of yield regulation, and also as a guide to silvicultural practice. The recognition of types is also of value in the selection of species (exotic or indigenous) for re-forestation. The boundaries of the units of management—series or compartments—should, as far as possible, be based on those of the forest types (Phillips, 1931*b*). Phillips (1928) gives a résumé of several conceptions of forest types. He points out that the various views "differ more in mode of expression than in reality. Thus, we find that those who lean towards a classification of types according to the community remember to consider the latter as indicators of habitat factors, whilst those who emphasize the physical basis do not fail to recognize the necessity of a knowledge of the vegetation differences."

Cajander (1926), who has done much work on the forest types of Finland, understands a type to be a community which when more or less mature has all its stands characterized by a similar or nearly similar ground flora, and he considers it feasible to use these forest types as a biological classification of localities without considering the species of trees. Phillips (1928) points out, however, that later on Cajander "records that investigations tend to show that the forest types reflect the properties of the soil so clearly that they satisfy to some extent the demands for a classification by which localities can be grouped naturally. Furthermore, the forest types afford a means whereby the classification of localities, according to the edaphic properties and the yields of the stands, can be harmonized."

When recognizing forest types during his work at Knysna in South Africa, Phillips (1928) had recourse to the floristics of the tree and shrub layers, to the growth form of the trees, and to the mean moisture content of the soil—this factor being reflected to some extent in the nature of the ground flora. He (Phillips, 1931*b*) considers a type as a threefold indicator—of past history, of present conditions, and of future possibilities.

During the cutting of the enumeration lines at Magamba it soon became apparent that there were considerable variations in the ground flora and undergrowth, and that to some extent there were corresponding variations in the dominant and co-dominant species. This factor was borne out when the actual enumeration was started, and it became evident that these changes in the vegetation could be more or less explained by differences of local climate, topography (aspect and altitude), soil moisture and human intervention. As the enumeration progressed it was realized that most of these communities

were generally so characteristic that it became no longer necessary to make notes on the ground flora and undergrowth, except in doubtful cases—usually transition zones. Difficulties, of course, were encountered, and it was by reference to the fuller notes then made that it was possible to decide to which community to assign the area in question.

Differences in the communities described above have been based mainly on the ground flora, and then on the undergrowth; it has also been shown on the one hand that there are differences in the habitat factors, and that on the other hand there are some corresponding differences in the dominant and co-dominant species. Most of these communities therefore might well be considered as "forest types", and it is suggested that their recognition will be of help to foresters both for regulating the yield, and for silvicultural practice, when bringing such a forest under systematic management.

Explanation of terms used

Association. The largest unit which consists of a definite assemblage of species (usually with definite dominants) and definite habitat.

Associes. A seral community with two or more dominants.

Climax community. A community in equilibrium with its environment.

Community. An assemblage of species irrespective of its rank.

Consociation. A community with a single dominant within an association.

Edaphic factors. The factors of the habitat which depend directly on the soil in which plants are rooted.

Habitat. The environment or the sum of the effective conditions under which a species or a community lives.

Hydrosere. The sere commencing in water or moist sites.

Lithosere. The sere commencing on bare rock.

Seral. Developmental, not climax.

Sere. A unit plant succession, comprising the development of a community from the pioneer stage to the climax.

Society. A community of lower rank in an association or consociation composed of subordinate species.

Subclimax. A seral community simulating a climax on account of its further development being inhibited by some disturbing factor such as clearing for cultivation.

Succession. The tendency for a community to change to another community until in equilibrium with its environment.

Xerosere. The sere commencing upon dry sites.

Summary

1. In the course of a survey on the basis of a 10% strip enumeration of warm temperate rain forest various communities of vegetation were recognized.

2. A brief description of the methods employed in the field is given.

3. A brief description of the topography, climate, geology and soils of the region covered is given.

4. The various synonyms for this type of forest are referred to briefly, and arguments are advanced in favour of the term "warm temperate rain forest".

5. Two seres, a hydrosere and a xerosere, were recognized and are described.

6. Two subseres, edaphic and biotic, are also recognized and described.

7. Descriptions are given of the forest and of the main communities, and reference made to variations within the communities.

8. In describing the communities the vegetation is divided up into four main storeys: dominants, second-storey trees, undergrowth and ground flora. The dominant storey can usually be subdivided in a silvicultural rather than a numerical sense into dominants, co-dominants and subdominants.

9. The possible ecological rank of each community is suggested, and the possible relationship between the communities is briefly referred to. This relationship is shown diagrammatically in Fig. 2.

10. The theory of forest types, its use and value, is discussed shortly, and it is suggested that most of the main communities described might well be considered to be forest types.

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APPENDIX I

Details of soil analyses by W. E. Carlton

No. of sample	Depth in inches	Horizon	Description	*p*H in H_2O	*p*H in KCl	Organic carbon	Gravel (over 2 mm.)	Clay composition % SiO_2	Fe_2O_3	Al_2O_3	Clay composition molec. ratios $\frac{SiO_2}{Al_2O_3}$	$\frac{SiO_2}{Fe_2O_3}$	$\frac{SiO_2}{R^*}$	$\frac{Al_2O_3}{Fe_2O_3}$
			Shallow podsolitic profile under temperate rain forest with ground flora											
2579	0–1	A0	Leaf litter	—	—	—	—	—	—	—	—	—	—	—
2580	1–5	A1	Leaf mould, entirely organic	3·15	2·5	—	—	—	—	—	—	—	—	—
2581	5–9	A1/A2	Friable loam with bleached quartz grains	3·25	2·8	15·6	13·8	14·5	9·3	12·2	2·00	4·12	1·35	2·05
2582	9–13	B2	Clayey loam, red-brown with rusty brown iron stone	4·2	3·8	4·2	57·9	23·9	21·0	21·1	1·93	3·04	1·18	1·58
2583	13–20	C1	Clayey loam, yellow-brown transitional layer	4·65	4·4	1·9	38·1	27·4	10·2	35·4	1·31	7·18	1·11	5·46
2584	20–28	C2	Rock decomposition layer	4·35	4·2	1·0	35·8	35·2	8·0	35·9	1·66	11·7	1·46	7·04
			Deep podsolized profile under temperate rain forest but with no ground flora											
2586	0–1	A0	Leaf litter	—	—	—	—	—	—	—	—	—	—	—
2587	1–6	A1	Leaf mould, entirely organic	3·0	2·35	—	—	—	—	—	—	—	—	—
2588	6–10	A1/A2	Friable loam with bleached quartz grains	3·4	2·95	13·7	32·1	19·5	9·5	15·5	2·13	5·45	1·53	2·55
2589†	10–16	B2	Loam, brown	4·35	3·8	7·3	26·5	21·8	15·4	21·5	1·73	3·77	1·18	2·19
2590	16–24	C1	Sandy loam, brown	4·6	4·3	3·3	27·2	28·2	11·9	27·9	1·72	6·30	1·35	3·67
2591	24–36	—	Pinkish buff decomposition layer	4·45	4·2	0·7	9·8	36·6	11·6	32·8	1·89	8·47	1·55	4·47
2592	36–48	C2	Salmon pink rock decomposition layer	4·2	4·05	0·2	7·3	—	—	—	—	—	—	—
2593	48–50	—	Pale pink rock decomposition layer	4·2	4·1	0·3	15·1	40·0	6·4	36·0	1·89	16·6	1·70	8·83
2594	52–58	—	Rotten rock fragments	—	—	—	—	—	—	—	—	—	—	—
			Laterized red earth under secondary bush											
2596	0–4	—	Plant debris	5·35	4·55	—	—	—	—	—	—	—	—	—
2597	4–12	—	Brownish black friable topsoil	5·95	5·1	—	—	—	—	—	—	—	—	—
2598	12–24	—	Dull brown moderately friable subsoil	5·05	4·35	—	—	—	—	—	—	—	—	—
2599	24–48	—	Similar to above layer	4·55	4·4	—	—	—	—	—	—	—	—	—
2600	48–60	—	Reddish brown somewhat clayey layer	4·75	4·55	—	—	—	—	—	—	—	—	—
2601	60–72	—	Rocky layer	4·6	4·35	—	—	—	—	—	—	—	—	—

* $R = Fe_2O_3 + Al_2O_3$.

† Sample 2589 also contains some A horizon material.

APPENDIX II

Alphabetical list of species with native names and frequencies in each community

The frequency in each community is indicated by the numbers 1–5 (see p. 61); frequencies in brackets indicate a low *constancy* of 1 or 2; 0 indicates only found in seral stages from heath.

Species	Native name	Family	Frequencies in communities 1–10									
			1	2	3	4	5	6	7	8	9	10
Trees—generally over 12 in. quarter girth:												
Adinandra schliebenii Melchior	Msambia No. 2	Theaceae	(1)	(2)	1	—	—	—	(1)	—	—	—
Albizzia gummifera (Gmel.) C. A. Smith	Mshai	Mimosaceae	—	—	—	(1)	—	2	—	—	—	—
Allophylus abyssinicus Hochst.	Mbangwe No. 2	Sapindaceae	—	—	—	(2)	—	2	—	—	—	—
Apodytes dimidiata E. Mey?	Mukanta	Icacinaceae	1	1	—	—	—	—	—	—	—	—
Bersama volkensii Gürke	Msindanguruwe	Myrsinaceae	1	—	—	1	—	—	1	1	—	—
Casearia sp. nr. C. engleri	Mtonte	Flacourtiaceae	1	(1)	—	—	—	—	—	—	—	—
Cassipourea elliottii Alston	Nekazito	Rhizophoraceae	1	—	—	(1–2)	1–2	—	1	—	—	—
Catha edulis Forsk.	Mwandama	Celastraceae	—	—	—	3	—	2	—	—	—	—
Chrysophyllum albidum G. Don.	Mbanasa	Sapotaceae	—	(1–2)	—	1–2	2–3	(1)	1–2	—	—	—
Clausena melliodes Hiern.	Mkunguni	Rutaceae	—	—	—	—	—	1	—	—	—	—
Cornus volkensii Harms.	Munyandege	Cornaceae	—	—	(1)	—	1	—	1	—	—	—
Craibia elliottii Dunn	Mhande	Papilionaceae	(1)	—	—	—	2	—	—	—	—	—
Croton sp. nr. C. scheffleri Pax.	Mshunduzi	Euphorbiaceae	(1)	—	—	1–2	—	1	1	—	—	—
Ekebergia rueppeliana A. Rich.	Mwonko	Meliaceae	—	—	—	1	—	—	—	—	—	—
Entandophragma sp.	Mbokoboko	,,	—	—	—	—	1	—	1	—	—	—
Faurea sp.	Msise	Proteaceae	½	(½)	—	—	—	—	—	—	—	—
Ficalhoa laurifolia Hiern.	Mkuka	Ericaceae	2	3	1	—	2	—	2–3	—	—	—
Ilex mitis (L.) Radlk.	Gendanamto	Aquifoliaceae	1	(1)	(1)	1	—	—	(1)	—	—	—
Lachnopylis sp.	Mvutiruanda	Loganiaceae	½	—	—	1	—	—	1	—	—	—
Macaranga kilimandscharica Pax.	Mkumba	Euphorbiaceae	3	2	2	2–3	5	2	2	2	—	—
*Mimusops sp.	Mugambo	Sapotaceae	—	—	—	(½)	—	—	—	—	—	—
*Mitragyna rubrostipulata (K. Sch.) Havil.	Mlombelombe	Rubiaceae	—	—	—	(½)	—	—	—	—	—	—
Ochna holstii Engl.	Mtakula	Ochnaceae	(2)	—	—	3	(1)	—	(2)	—	—	—
Ochrocarpus africanus Oliv.	Msambia No. 1	Guttiferae	—	(1)	—	—	—	—	(1)	—	—	—
Ocotea usambarensis Engl.	Mkulo	Lauraceae	5	4	3–4	3	3	—	3	5	—	—
Olea hochstetteri Bak.	Ngwe	Oleaceae	1	—	—	(1)	—	—	(1)	—	—	—
*Parinarium holstii Engl. (nomen)	Mkula	Rosaceae	—	—	—	(½)	—	—	—	—	—	—
Pittosporum abyssinicum Hochst.	Mbuzungu	Pittosporaceae	—	—	—	—	—	—	(1)	½	—	—
Podocarpus gracilior Pilg.	Msee	Taxaceae	(1)	—	—	(1)	1	—	—	—	—	—
P. milanjianus Rendle	,,	,,	(4)	3	4	(1)	4	—	3–4	—	—	—
P. usambarensis Pilg.	,,	,,	—	—	—	1	½?	—	2	—	—	—
Polyscias kikuyuensis Summerhayes	Mfumbati No. 1	Araliaceae	—	—	—	—	1	2	—	—	—	—
Pygeum africanum Hk. f.	Mkomohoyo	Rosaceae	1	1	1–2	1	1	1–2	2	—	—	—
Rapanea usambarensis Gilg. & Schel.	Mshuizo	Myrsinaceae	3	(1)	(2)	2	—	—	2	1	—	—
Strombosia sp.	Mshumba	Olacaceae	1	(1)	—	—	1	—	(1)	—	—	—
Syzygium cordatum Hochst.	Mshiwi	Myrtaceae	2–3	2	2–3	(1)	2	—	2	1	—	—
Teclea nobilis Del.	Kilongolo	Rutaceae	2	(1)	—	1–2	2	—	1–2	1–2	—	—

* Maximum altitude about 1650 m.

APPENDIX II (*contd.*)

Species	Native name	Family	1	2	3	4	5	6	7	8	9	10
			Frequencies in communities 1–10									
TREES—generally under 12 in. quarter girth:												
Agauria salicifolia Hk. f.	Mwandari	Ericaceae	0	—	—	—	—	—	—	—	—	—
Aphloia myrtiflora Galp.	Mdananda	Flacourtiaceae	—	2	—	2	2	—	(1)	2	—	—
Apocynaceae, species of	Kireiti	Apocynaceae	—	—	—	(1)	—	—	—	—	—	—
Araliaceae, species of	Mfumbati No. 2	Araliaceae	2	(1)	2	—	2	—	3	2	—	—
Canthium sp.	Mdalia	Loganiaceae	—	(1)	—	—	—	—	(1)	—	—	—
Conopharyngia sp.	Mkoko	Apocynaceae	—	—	—	(1)	2	—	(1–2)	1–2	—	—
Cussonia spicata	Tenderi	Araliaceae	—	—	—	(1)	—	2	—	—	—	—
Dasylepis leptophylla Gilg.	Kigwande	Flacourtiaceae	(2)	(2)	(1)	2	2	—	3	—	—	—
Dombeya leucoderma K. Schum.	Mkeyu	Sterculiaceae	—	—	—	—	—	3	(1)	—	—	—
Euclea sp.	Muhangazunga	Ebenaceae	—	—	—	—	—	(1)	—	—	—	—
Gymnosporia lepidota Loes. "var. kilimandscharicus"	Mamata	Celastraceae	(1)	(1–2)	(2)	(½)	(2)	—	(1)	—	—	—
Ixora albersii K. Schum.	Mquingwa No. 1	Rubiaceae	—	—	—	(1)	—	—	—	—	—	—
Lachnopylis holstii (Gilg.) C. A. Smith	Mwashi	Loganiaceae	(½)	—	—	—	—	—	—	—	—	—
Maesa lanceolata Forsk.	Mteri	Myrsinaceae	—	—	—	—	—	3	—	—	—	—
Myrica kilimandscharica Engl.	Mshegeshi	Myricaceae	0	—	—	—	—	—	—	—	—	—
Oxyanthus speciosus DC.	Mquingwa No. 2	Rubiaceae	—	—	—	(½)	—	—	—	—	—	—
Peddiea fischeri Engl. P. volkensii Gilg.	Mkisigize	Thymelaeaceae	—	—	—	(½)	—	—	—	—	—	—
Ritchiea albersii Gilg.	Mwozanyama	Capparidaceae	—	—	—	—	—	(½)	—	—	—	—
Sclopia sp. v.n. stuhlmannii	Mhongora	Flacourtiaceae	—	—	—	(½)	—	—	—	—	—	—
Teclea grandifolia Engl.	?Mquati	Rutaceae	(1)	—	(1)	2	(1)	—	—	½	—	—
Trema guineensis Ficalho	Mshinga	Ulmaceae	—	—	—	—	—	(1)	—	—	—	—
Trichelia volkensii Gürke	Mbangwe No. 1	Meliaceae	—	—	—	—	—	—	—	½	—	—
Trichocladus malosanus Bak.	Mkombeti	Hamamelidaceae	(3)	1	(2)	—	1	—	—	—	—	—
Vangueria edulis Vahl.	—	Rubiaceae	—	—	—	—	—	(1)	—	—	—	—
Xymalos monospora Baill.	Mdimudimu	Monimiaceae	—	—	—	1	—	—	—	1	—	—
SHRUBS:												
Berberis holstii Engl.	—	Berberidaceae	—	—	—	—	—	—	—	—	(1)	—
Chasalia (or Psychotria)	Huyu No. 4	Rubiaceae	—	—	—	(4)	—	—	—	—	—	—
Clausena anisata Oliv.	Mjavikari	Rutaceae	(½)	—	—	—	—	—	—	—	—	—
Cluytia mollis Pax.	Muhende	Euphorbiaceae	—	—	—	—	—	(1)	—	—	—	—
Cyathea usambarensis Hiern.?	—	Cyatheaceae	—	4–5	(2)	—	(2)	—	—	—	—	—
Dodonaea viscosa L.	Mzutwe	Sapindaceae	0	—	—	—	—	(2)	—	—	3	—
Dracaena papahu Engl.	—	Liliaceae	—	—	—	(2)	—	(1–2)	—	—	—	—
Grumilea buchananii K. Schum.	Kelampindi No. 1	Rubiaceae	(3)	(3–4)	3	—	—	—	(1)	—	—	—
G. platyphylla K. Schum.	,, No. 2	,,	—	—	—	(2)	(1)	3	3	—	—	—
Gymnosporia sp.	Mtindakunguru	Celastraceae	(½)	—	—	—	—	—	—	—	—	—
Halleria lucida L.	Mkungalunga	Scrophulariaceae	—	—	—	—	—	—	(2)	—	—	—
Hypericum lanceolatum Lam.	Mwambaziwa	Hypericaceae	—	—	—	—	—	—	—	—	—	4
Lasianthus kilimandscharicus K. Schum.	Huyu No. 2	Rubiaceae	(4)	(3)	(2)	1	4	—	—	2	—	—
Lasianthus sp.nov.	,, No. 1	,,	4–5	4	4	—	2	—	(1)	4	—	—
Lobelia (giant)	—	Lobeliaceae	—	—	—	—	—	(2)	—	—	—	—
Maba natalensis Harv.	Kihagiro No. 3	Ebenaceae	—	—	—	(1)	—	—	—	—	—	—

Species	Native name	Family	Frequencies in communities 1–10: 1	2	3	4	5	6	7	8	9	10
Memecylon sp.	Kihagiro No. 1	Melastomaceae	(3–4)	(2)	2	—	—	—	—	—	—	—
Moustea grandiflora Gilg.	,, No. 2	Scrophulariaceae	—	(1)	—	(1)	—	—	—	—	—	—
Pavetta dalei Brem.	Huyu No. 3	Rubiaceae	—	—	(1)	(2–3)	—	4	4	2	—	—
Philippia holstii Engl.	Msheruti	Ericaceae	—	—	—	—	—	—	—	—	5	—
Piper capensis L.	—	Piperaceae	—	—	—	—	—	(3)	(2)	—	—	—
Psychotria alsophila K. Schum.	Kajisokakungu	Rubiaceae	(1)	—	—	2	—	—	—	—	—	—
P. engleri K. Kr.	—	,,	—	(1)	—	—	—	—	—	—	—	—
Psychotria sp. (No. 404)	—	,,	(1)	(2)	2	—	(2)	—	2	—	—	—
Psychotria (see Chasalia)	—	,,	—	—	—	—	—	—	—	—	—	—
Rhamnus prinoides L'Hérit.	Msheshewi	Rhamnaceae	—	—	—	(2)	—	—	—	—	2	—
Smithia mildbraedii Harms.	—	Papilionaceae	—	—	—	—	—	—	—	—	2	—
Solanum sp. nr. S. schumannianum Dam.	Mjujuri	Solanaceae	—	—	—	—	—	3	—	—	—	—
Urophyllum holstii K. Schum.	Huyu No. 5	Rubiaceae	(3)	—	(2)	—	2	—	—	2	—	—
SUBSHRUBS AND HERBS, etc.:												
Acanthaceae, species of	Mshikise	Acanthaceae	—	(1)	5	5	2	4–5	—	5	—	—
Composite species (in swamps)	—	Compositae	—	—	—	—	—	—	—	—	—	4
Coreopsis sp. nr. C. steppia	Segimbi	,,	—	—	—	—	—	—	(2)	—	(1)	—
Crassulaceae, species of (on cliffs)	—	Crassulaceae	—	—	—	—	—	—	(1)	—	—	—
Creepers	—	—	—	—	—	2	—	4	—	—	—	—
Crossandra tridentata Lindau	—	Acanthaceae	—	—	—	—	(5)	—	—	—	—	—
Cyperaceae, species of	—	—	—	—	—	—	—	—	—	—	—	5
Dryopteris gongylodes (Sch.) O. Ktze.	—	Filicales	—	—	—	—	—	—	—	—	—	5
Epiphytes	—	—					Not recorded					
Erlangea sp.	—	Compositae	—	—	—	—	—	(4)	—	—	—	—
Ferns	—	—					Not recorded					
Gramineae, species of	—	Gramineae	—	—	—	(1)	—	—	—	—	—	—
Impatiens pseudoviola Gilg.	—	Balsaminaceae	—	—	5	—	—	—	—	—	—	—
Impatiens sp. (large) splendens?	—	,,	—	5	—	—	—	—	—	—	—	—
Isoglossa lactea Lindau	Mshikise	Acanthaceae	—	—	—	—	5	—	—	—	—	—
Lianes	—	—	—	—	—	2	—	4	—	—	—	—
Lichens	—	—					Not recorded					
Lobelia sp. (small)	—	Lobeliaceae	—	—	—	—	—	—	—	—	3	—
Lycopodium sp.	—	Lycopodiaceae	—	—	—	—	—	—	—	—	4	—
Mosses	—	—					Not recorded					
Orchid	—	Orchidaceae	—	—	—	—	—	—	—	—	3	—
Pennisetum sp.	—	Gramineae	—	—	—	—	—	—	—	—	—	5
Pilea sp. v. nr. P. engleri	—	Urticaceae	—	—	4	—	—	—	—	—	—	—
Pteridium aquilinum Kuhn	—	Filicales	—	—	—	—	—	—	—	—	4	—
Rubus sp.	—	Rosaceae	—	—	—	—	—	4	—	—	—	—
Salvia? sp.	—	Labiatae	—	—	(3)	—	—	—	—	—	—	—
Selaginella sp.	—	Selaginellaceae	—	—	—	(1)	—	—	—	—	—	—
Typha sp.	—	Typhaceae	—	—	—	—	—	—	—	—	—	5

APPENDIX III

Alphabetical list of native (Kisambaa) names and botanical equivalents

Gendanamto	Ilex mitis (L.) Radlk.
Huyu No. 1	Lasianthus sp.nov.
,, No. 2	L. kilimandscharicus K. Schum.
,, No. 3	Pavetta dalei Brem.
,, No. 4	Psychotria or Chasalia?
,, No. 5	Urophyllum holstii K. Schum.
Kajisokakungu	Psychotria alsophila K. Schum.
Kelampindi No. 1	Grumilea buchananii K. Schum.
,, No. 2	G. platyphylla K. Schum.
Kigwande	Dasylepis leptophylla Gilg.
Kihagiro No. 1	Memecylon sp.
,, No. 2	Moustea grandiflora Gilg.
,, No. 3	Maba natalensis Harv.
Kilongolo	Teclea nobilis Del.
Kireiti	? Apocynaceae
Kuti	Chrysophyllum albidum G. Don.
Mamata	Gymnosporia lepidota Loes. "var. kilimandscharicus"
Mbamba	—
Mbanasa	Chrysophyllum albidum G. Don.
Mbangwe No. 1	Trichelia volkensii Gürke
,, No. 2	Allophylus abyssinicus Hochst.
Mbokoboko	Entandophragma sp.
Mbuzungu	Pittosporum abyssinicum Hochst.
Mdalia	Canthium sp.
Mdananda	Aphloia myrtiflora Galp.
Mdimudimu	Xymalos monospora Baill.
Mfumbati No. 1	Polyscias kikuyuensis Summerhayes
,, No. 2	? Araliaceae
Mgoma	Chrysophyllum albidum G. Don.
Mhande	Craibia elliottii Dunn
Mhongora	Sclopia sp. v. nr. stuhlmannii
Mjavikari	Clausena anisata Oliv.
Mjujuri	Solanum sp. nr. S. schumannianum Dam.
Mkeyu	Dombeya leucoderma K. Schum.
Mkisigize	Peddiea fischeri Engl.
Mkoko	Conopharyngia sp.
Mkombeti	Trichocladus malosanus Bak.
Mkomohoyo	Pygeum africanum Hk. f.
Mkuka	Ficalhoa laurifolia Hiern.
Mkula	Parinarium holstii Engl.
Mkulo	Ocotea usambarensis Engl.
Mkumba	Macaranga kilimandscharica Pax.
Mkungalunga	Halleria lucida L.
Mkunguni	Clausena melliodes Hiern.
Mlifu	—
Mlombelombe	Mitragyna rubrostipulata (K. Sch.) Havil.
Mlungu	—
Monko	Ekebergia rueppeliana A. Rich.
Mquati	Teclea grandifolia Engl.
Mquingwa No. 1	Ixora albersii K. Schum.
,, No. 2	Oxyanthus speciosus DC.
(Mrosirosi)	Hagenia abyssinica*
Msambia No. 1	Ochrocarpus africanus Oliv.
,, No. 2	Adinandropsis sp.nov.
Msee	Podocarpus all species
Mshai	Albizzia gummifera (Gmel.) C. A. Smith
Mshegeshi	Myrica kilimandscharica Engl.
Msheruti	Philippia holstii Engl.
Msheshew	Rhamnus prinoides L'Hérit.
Mshikise	Various Acanthaceae
Mshinga	Trema guineensis Ficalho

* Probably introduced by the Germans from other parts of the Territory.

Mshiwi	Syzygium cordatum Hochst.
Mshuizo	Rapanea usambarensis Gilg. & Schel.
Mshumba	Strombosia sp.
Mshunduzi	Croton sp. nr. C. scheffleri Pax.
Msindanguruwe	Bersama volkensii Gürke
Msise	Faurea sp.
Msumba	—
Mtakula	Ochna holstii Engl.
Mteri	Maesa lanceolata Forsk.
Mtindakunguru	Gymnosporia sp.
Mtonte	Casearia sp. nr. C. engleri
Mugambo	Mimusops sp.
Muhangazunga	Euclea sp.
Muhende	Cluytia mollis Pax.
Mukanta	Apodytes sp. perhaps dimidiata E. Mey.
Munyandege	Cornus volkensii Harms.
Mvilu	—
Mvutiruanda	Lachnopylis sp.
Mwambaziwa	Hypericum lanceolatum Lam.
Mwandama	Catha edulis Forsk.
Mwandari	Agauria salicifolia Hk. f.
Mwashi	Lachnopylis holstii (Gilg.) C. A. Smith
Mwombola	Agauria salicifolia Hk. f.
Mwonko	Ekebergia rueppeliana A. Rich.
Mwozanyama	Ritchiea albersii Gilg.
Mzusu	Mimusops sp.
Mzutwe	Dodonaea viscosa L.
Nekazito	Cassipourea elliottii Alston
Ngwo	Olea hochstetteri Bak.
Sogimbi	Coreopsis sp. nr. C. steppia
Tenderi	Cussonia spicata

SOME OBSERVATIONS ON THE EPIPHYTIC MOSS FLORA OF TREES IN ARGYLL

By N. MARY MARTIN

(*With one Figure in the Text*)

CONTENTS

INTRODUCTION

THE purpose of this investigation, carried out in July 1934, was the comparative study of the moss flora on different species of trees growing under different environmental conditions. The locality chosen, Achnacloich in Argyll, is very favourable for the study of epiphytic bryophytes and lichens on account of the oceanic conditions, cool winds and heavy rainfall, which persist through most of the year, as the prevailing moisture-carrying west winds come in from the Atlantic. The district round Achnacloich is very well wooded, extensive plantations being in existence on the Achnacloich estate, as well as much wood which appears natural. The state forest (Fearnoch Forest) is slightly to the south-east of Achnacloich. The great amount of free water in the neighbourhood, in the form of lochs, rivers and burns of all sizes, and the dense wood, allied to and correlated with the heavy rainfall make a remarkably suitable habitat for mosses on the trees. The moss covering is in some cases quite extraordinary, and on some of the oaks moss and lichen together cover the entire bark, from quite small twigs down to the base of the trunk.

The results of the investigation given below are for mosses only. Specimens of lichens and leafy liverworts were taken at the same time, and statistics as to their occurrence and frequency obtained in similar detail to those for mosses, but these results have not yet been worked out.

Trees of different species were chosen, and an attempt was made to study them in different habitats. Detailed observations were made for each individual tree studied, including the average height and diameter, the altitude (as shown

on the 6 in. to the mile Ordnance Survey sheet), the exposure to the prevailing wind, and the zonation of the moss species both up and round the trunk: finally the species present were listed and their distribution on the tree noted. The lists were not meant to be exhaustive; some care was taken to collect samples of all mosses which were unknown, but there was no search for rare specimens as such.

Various trees were selected for investigation. Special attention was paid to oaks (of which the vast majority were *Quercus robur*) since they appeared to form natural woodland and further since they were evidently affected to a considerable extent by exposure.

Quercus

Out of the 227 trees investigated 81 were oaks, two of these having characters intermediate between *Q. robur* and *Q. sessiliflora*, the other 79 being *Q. robur*. Their habitats varied from a completely sheltered valley to completely exposed situations on the ground bordering Loch Etive.

In the completely sheltered situations little bark was to be seen owing to the heavy moss covering even on quite young trees, but as the exposure to prevailing winds increased the moss covering became markedly scantier both in thickness and extent and if there was any zonation this tended to be compressed downwards. There was no evidence that mosses preferred the side away from the wind, although on a few occasions there was not quite so much moss on the southern side of a trunk when that side was fully exposed to sun.

In Table I, which shows the total list of moss species found on oaks, column 1 shows the percentage of trees on which each moss was found. It will be seen that *Hypnum cupressiforme*, with its variety *filiforme*, *Eurhynchium myosuroides*, *Dicranum scoparium* and *Thuidium tamariscinum* are found most frequently. An interesting addition is seen in *Pylaisia* (*Leskea*) *polyantha*, a somewhat rare moss which grows on trees and which is found here as a colonist with *Ulota crispa*.

Table I also shows the effect of exposure upon the moss flora in the remaining columns. Attention may be called to the group of mosses marked with an asterisk, which show their highest frequencies for sheltered trees and decrease as the exposure increases. These are all mosses of the woodland carpet and occur only on the bases of the trees. The two species of *Mnium* represented, *Mn. hornum* and *Mn. affine*, both show their highest values in the "open to the prevailing wind" category. It may be (Bowen, 1931, 1933) that the better internal conducting system of this genus makes them more able to withstand a certain amount of exposure, particularly as they are only found round the base of trees, and that in the more sheltered situations they are crowded out by more luxuriant ground forms, such as species of *Dicranum*, *Thuidium* and *Hylocomium*. An analogy may perhaps be found in the behaviour of *Mnium hornum* in the Chiltern Plateaux woods (Watt's C type) which appears on the

Table I. Quercus robur. *Effect of exposure to prevailing winds. Moss frequencies expressed as percentages of trees on which each moss occurred*

Moss species	Frequency on trees collectively	Frequency on trees sheltered	On trees *not* open to west	On trees open to west	On exposed trees
Hypnum cupressiforme var. filiforme	92·6	100·0	86·8	86·8	100·0
Eurhynchium myosuroides	80·2	75·0	100·0	95·7	47·4
Hypnum cupressiforme	60·5	43·8	65·1	78·2	52·6
Ulota crispa	40·7	18·8	34·7	34·7	73·7
*Dicranum scoparium	25·9	43·8	30·4	17·4	15·8
*Thuidium tamariscinum	24·7	75·0	17·4	4·3	15·8
Mnium hornum	17·3	12·5	8·7	43·4	5·3
Pylaisia polyantha	15·6	—	13·0	17·4	31·6
Camptothecium sericeum	12·4	—	26·0	13·0	5·3
*Eurhynchium myurum	8·6	6·3	21·7	43·4	—
Mnium affine	6·2	—	4·3	13·0	5·3
*Hylocomium splendens	5·0	18·8	—	—	5·3
*H. loreum	3·7	12·5	4·3	—	—
*Plagiothecium undulatum	3·7	12·5	4·3	—	—
*Hylocomium brevirostre	2·5	6·3	4·3	—	—
Brachythecium purum	2·5	—	4·3	—	5·3
*B. rutabulum	1·2	—	4·3	—	—
*Hypnum Schreberi	1·2	—	4·3	—	—
Polytrichum formosum	1·2	—	—	—	5·3
No. of trees in each category	81	16	23	23	19

Increasing exposure to the prevailing wind (west). ——————————→

fringe of beechwoods in these situations. Watt (1934) suggests that this is a wind effect, the wind carrying away the litter and thus clearing the ground upon which *Mnium* can then establish itself.

The high frequencies of *Hypnum cupressiforme* var. *filiforme*, *H. cupressiforme* type and *Eurhynchium myosuroides* may also be noted, the first named rising to 100% on sheltered and exposed trees, and *Eurhynchium* decreasing with exposure. The very high percentage of *Ulota crispa* on the exposed trees may be correlated with its habit, since it is an acrocarpous moss, each shoot being rooted to the bark. *Pylaisia* also has a relatively high percentage on exposed trees and has prostrate, rooting shoots.

Zonation. The normal type of zonation may be seen on the left-hand side of the two trees shown in the accompanying diagram (Fig. 1). The right-hand side of these trees shows the effect of exposure on zonation and distribution of species of moss. From the base upwards the typical zones on a tree with splayed-out base in a sheltered situation are: *Eurhynchium, Hypnum cupressiforme, H. cupressiforme* var. *filiforme* and finally *Ulota* and *Pylaisia.* As may be seen from the diagram, however, there are certain variations from the normal. Zones may be omitted as a result of exposure and they may have an admixture of other species. Further when one side of a trunk, or the whole trunk, reaches ground level while still vertical, i.e. when the lower portion of the trunk is not splayed out, *Hypnum cupressiforme* var. *filiforme* is very frequently found right down to ground level. The mosses of the ground flora always tend to overgrow the outspread roots or the splayed-out base of a trunk. In such

cases they either form a zone below the *Eurhynchium* or are found mixed with it and *Hypnum cupressiforme* in the basal zone.

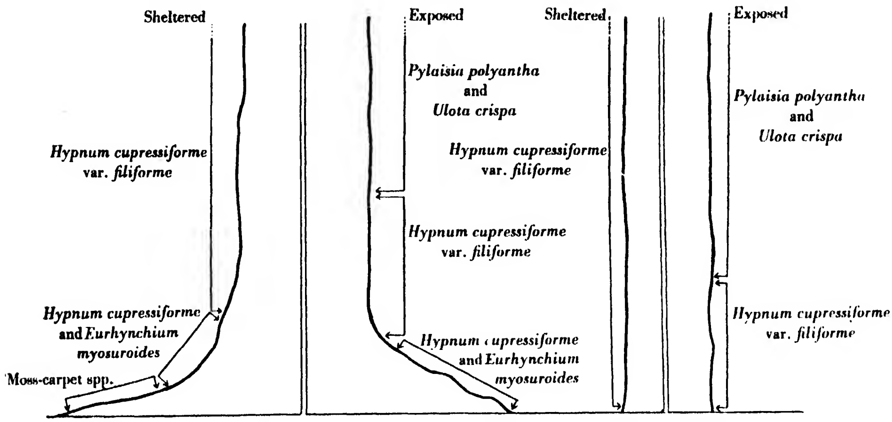

FIG. 1. Diagram to show distribution of species and zonation due to exposure. The left-hand diagram shows the zonation on a sheltered (left) and an exposed (right) tree of large size; and the right-hand diagram the same contrast in the case of a smaller tree.

The first two columns in Table II, which show the comparison of species found upon unzoned and zoned trees, have several interesting features. The four species found most commonly upon the sheltered, and upon the clearly

Table II. Quercus robur

Moss species	Comparison of frequencies: Unzoned trees		Zoned trees	Frequencies in the various zones: Zone 1 (basal)	Zone 2	Zones 3 and 4
Hypnum cupressiforme var. filiforme	73·7	→	96·9	9·7	71·0	61·5
Eurhynchium myosuroides	52·6	→	87·1	85·5	6·4	—
Hypnum cupressiforme	26·3	→	71·0	51·6	21·0	—
Ulota crispa	84·2	←	25·8	—	11·3	42·3
Dicranum scoparium	5·3	→	32·3	22·6	8·0	3·9
*Thuidium tamariscinum	—		30·7	30·7	1·6	—
Mnium hornum	5·3		21·0	22·6	—	—
Pylaisia polyantha	21·1	←	13·0	—	9·7	15·4
Camptothecium sericeum	31·6	←	6·4	3·2	3·2	—
*Eurhynchium myurum	—		11·3	11·3	—	—
Mnium affine	5·3		6·4	6·4	—	—
*Hylocomium splendens	—		6·4	6·4	—	—
*H. loreum	—		4·8	4·8	—	—
*Plagiothecium undulatum	—		4·8	4·8	—	—
*Hylocomium brevirostre	—		3·2	3·2	—	—
*Brachythecium purum	—		3·2	3·2	—	—
*B. rutabulum	—		1·6	—	1·6	—
*Hypnum Schreberi	—		1·6	1·6	—	—
*Polytrichum formosum	—		1·6	1·6	—	—
No. of trees in each category	19		62	26 of the 62 zoned trees had more than 2 zones		

* Mosses of the basal zone of zoned trees only, i.e. only in most sheltered position. Usually wood-carpet species.

zoned trees (*H. cupressiforme* var. *filiforme*, *Eurhynchium*, *Hypnum cupressiforme* and *Dicranum scoparium*) are found in far higher percentages upon the zoned than upon the unzoned trees, while those two species which normally form the top zone in a tree with several zones, i.e. *Ulota crispa* and *Pylaisia polyantha*, together with *Camptothecium sericeum*, are found in greater percentage upon the unzoned trees. A further point of interest is that those mosses absent from the unzoned trees are found in the basal zone of the zoned trees and are mainly mosses of the wood carpet which have overflowed under favourable conditions on to the lower parts of the trunk.

The remaining columns of Table II give the frequency of the mosses present in the different zones. Again it is evident that the mosses in the basal zone and absent from any zone above are for the most part moss-carpet species. Even though from this table it is clear that *Ulota crispa* and *Pylaisia polyantha* increase from the basal zone upwards, there is one obvious failure of the table. Some mosses may be represented in a second zone, but coming from a two-zoned tree that zone really corresponds with Zone 4 of a four-zoned tree, or Zone 3 of a three-zoned tree. Table III was therefore drawn up in which the

Table III. Quercus robur

	Two-zoned trees		Three-zoned trees		
Moss species	Zone 1	Zone 2	Zone 1	Zone 2	Zone 3
Eurhynchium myosuroides	83·3	2·8	86·4	9·1	—
Hypnum cupressiforme	69·4	5·6	27·2	40·8	—
Thuidium tamariscinum	33·3	—	18·2	—	—
Dicranum scoparium	25·2	11·1	13·6	4·5	—
Mnium hornum	25·2	—	13·6	—	—
Hypnum cupressiforme var. filiforme	8·4	88·9	13·6	40·8	59·1
Camptothecium sericeum	5·6	—	—	4·5	—
Pylaisia polyantha	—	11·1	—	4·5	13·6
Ulota crispa	—	13·9	—	9·1	36·4
Eurhynchium myurum	19·5	—	—	—	—
Brachythecium purum	5·6	—	—	—	—
Hylocomium brevirostre	2·8	—	—	—	—
Plagiothecium undulatum	5·6	—	4·5	—	—
Hylocomium splendens	8·4	—	—	—	—
H. loreum	2·8	—	—	—	—
Mnium affine	—	—	13·6	—	—
Brachythecium rutabulum	—	—	—	4·5	—
Polytrichum formosum	—	—	4·5	—	—
No. of trees in categories	36 two-zoned trees		22 three-zoned trees		

trees are split up into these different categories. Unfortunately this results in low numbers which increase the inaccuracy of percentages. This was so marked in the case of four-zoned trees (of which there were only four) that that category has been omitted although the results pointed in the same direction (see p. 87). It will be clearly seen from columns 1 and 2 of Table III which deal with two-zoned trees, that only *Hypnum cupressiforme* var. *filiforme*, *Pylaisia* and *Ulota* increase in Zone 2 and they do so most markedly, whereas the other species present are most frequent in Zone 1, the basal zone.

The remaining columns for three-zoned trees show this increase very clearly, for all these three mosses are most frequent on the trunk of the tree, while *Eurhynchium* is seen to be commonest in Zone 1 and *Hypnum cupressiforme* in Zone 2. These two latter mosses occupy the same position on four-zoned trees while the chief constituent of Zone 3 is *H. cupressiforme* var. *filiforme*, and of Zone 4 *Pylaisia* and *Ulota*, which occur in no other zone.

Table IV shows the correlation of zonation with exposure. This is seen very clearly in *Quercus robur*. All the sheltered trees were found to be zoned, and less than half the exposed trees were zoned.

Table IV. Quercus robur. *Correlation of zonation with exposure. Expressed as percentages*

	Sheltered	Open, *not* to west	Not exposed	Open to west	Exposed	Exposed
Zoned	100	91·3	94·9	74·9	42·1	59·5
Unzoned	0	8·7	5·1	25·1	57·9	40·5
Actual number of trees studied	16	23	39	23	19	42

Fraxinus

Only 38 trees of *Fraxinus excelsior* were studied and this has undoubtedly affected the results. Nevertheless they afford some degree of comparison with the results for *Quercus*. The most marked difference is the great increase in the percentages of *Ulota crispa*, *Pylaisia polyantha* and *Camptothecium sericeum*, as compared with their values upon *Quercus*. Further reference to these differences will be made later.

In studying the effect of exposure upon the floristic the badly distributed numbers tell heavily. Only four trees "open but not to the west", and only three trees "open to the west" were studied, as compared with twelve "sheltered" and nineteen "exposed" trees. This inequality of numbers was unfortunate and the resulting percentages only give a very approximate idea of the frequencies under these conditions.

For this reason Table V was drawn up giving percentages for two categories only, trees exposed to the prevailing wind ("open to the west", and "exposed" trees together) and trees not exposed to the prevailing wind ("sheltered", and "open but not to the west").

Table V. Fraxinus excelsior. *Showing effect of exposure on moss flora*

Moss species	Trees collectively	Trees *not* exposed to prevailing wind	Trees exposed to prevailing wind (west)
Hypnum cupressiforme	84·2	100	72·7
Ulota crispa	78·9	75·0	76·0
Hypnum cupressiforme var. filiforme	78·9	93·8	68·2
Pylaisia polyantha	44·7	56·2	36·4
Eurhynchium myosuroides	44·7	68·8	27·3
Camptothecium sericeum	39·5	37·5	40·9
Thuidium tamariscinum	21·0	43·8	4·5
Eurhynchium myurum	21·0	50·0	—
Mnium hornum	10·5	18·8	4·5
Brachythecium rutabulum	7·9	12·5	4·5
Hylocomium brevirostre	7·9	18·8	—
Mnium affine	5·3	6·3	4·5
Dicranum scoparium	5·3	6·3	4·5
Neckera complanata	5·3	6·3	4·5
Brachythecium salebrosum	5·3	12·5	—
Hylocomium triquetrum	2·6	6·3	—
H. squarrosum	2·6	6·3	—
Hypnum Schreberi	2·6	6·3	—
Bryum sp.	2·6	—	4·5
No. of trees studied	38	16	22

Zonation. It was again found (see Table VI) that those mosses missing from the unzoned trees were present in the basal zone of the zoned and were moss-carpet species. Such species stand little chance of getting on to unzoned trees since they are absent from the moss carpet which is much sparser or absent in those situations in which unzoned trees are commonly found.

Table VI. Fraxinus excelsior

Moss species	Comparison of moss frequencies on unzoned and zoned trees			Moss frequencies in the various zones				
	Unzoned		Zoned	Zone 1 (basal)		Zone 2		Zone 3
Hypnum cupressiforme	81·8	→	88·5	80·8	←	11·5	←	—
H. cupressiforme var. filiforme	63·6	→	88·5	15·4		73·0		66·6
Ulota crispa	81·8		80·8	23·0	→	57·7	→	66·6
Pylaisia polyantha	45·5	→	50·0	19·3		34·6		—
Eurhynchium myosuroides	54·6		42·3	42·3	←	7·7	←	—
Camptothecium sericeum	45·5	←	38·5	30·8	←	3·9	←	—
*Thuidium tamariscinum	—		30·8	26·9		3·9		—
Eurhynchium myurum	18·2		23·0	19·3		7·7		—
*Mnium hornum	—		15·4	15·4		—		—
*Hylocomium brevirostre	—		11·5	11·5		—		—
*Dicranum scoparium	—		7·7	7·7		—		—
*Mnium affine	—		7·7	7·7		—		—
*Neckera complanata	—		7·7	3·9		3·9		—
*Brachythecium rutabulum	—		7·7	7·7		—		—
*B. salebrosum	—		7·7	7·7		—		—
*Bryum sp.	—		3·9	3·9		—		—
*Hylocomium triquetrum	—		3·9	3·9		—		—
*H. squarrosum	—		3·9	3·9		—		—
*Hypnum Schreberi	—		3·9	—		—		11·5
No. of trees in each category	11		26 (1 tree had no moss at all)	9 of the 26 trees had more than two zones				

* Moss-carpet species found in basal zone only—except the single specimen of *Hypnum Schreberi*.

There is little difference in the percentages of *Ulota crispa*, *Camptothecium sericeum* and *Pylaisia polyantha*, but these mosses show a very high percentage on all ash trees, whether zoned or unzoned, in contrast to their behaviour on oaks, where they are much more frequent on unzoned trees. In the comparison of mosses from the different zones *Ulota* alone shows its highest frequency in the top zone, while *Pylaisia* and *Hypnum cupressiforme* var. *filiforme* show their highest frequency in the second zone.

In the analysis of the zones in two-zoned and three-zoned trees separately the behaviour of *Hypnum cupressiforme*, *Ulota crispa* and *Hypnum cupressiforme* var. *filiforme* is of most interest and is much the same as in oaks, i.e. on two-zoned trees *H. cupressiforme* type is found most frequently in the basal zone, while the variety *filiforme* and *Ulota* are found chiefly in the second zone. In three-zoned trees *Ulota* is the type species for the top zone, *Hypnum cupressiforme* var. *filiforme* for the second zone, and *H. cupressiforme* for the basal zone.

The correlation of zonation with exposure is nothing like so clear as in oak, but it seems (Table VII) that a slightly greater proportion of trees are unzoned than zoned when exposed to the prevailing wind.

Table VII. Fraxinus excelsior. *Correlation of zonation with exposure. Expressed as percentages*

	Sheltered	Open, *not* to west	Sheltered + Open, *not* to west: Not exposed	Open to west	Exposed	Open to west + Exposed: Exposed
Zoned	83·3	50·0	75·0	33·3	68·4	63·6
Unzoned	16·6	50·0	25·0	66·6	31·6	36·4
Actual number of trees studied	12	4	16	3	19	22

One interesting point in connexion with the moss covering of the ash trees is the occurrence of *Ulota crispa* in Zone 1, a state of affairs which is probably due to the less dense covering of the ash trees as compared with oaks allowing colonizers to persist lower down the trunk. (*Ulota* was found in Zone 1 of 6 trees.) Further discussion of these differences will be found in the section dealing with the autecology of the mosses and the reasons for the varying distribution of the mosses upon the different species of tree.

Betula and other species

Of the other trees studied 28 were *Betula alba*, 22 *Acer pseudoplatanus*, 12 *Fagus sylvatica* and 18 conifers. None of these were studied in sufficient numbers to enable valuable comparisons to be made of the effect of exposure on the floristic and on zonation.

Table VIII gives a comparison of the moss frequencies upon all these trees. The results for the different trees are not, however, strictly comparable. For example, for oaks and ashes the percentages of exposed trees were different.

Table VIII. *Comparison of floristic on different species of trees. Expressed as percentages*

Moss species	*Quercus* (81)	*Fraxinus* (38)	*Betula* (28)	*Acer* (22)	*Fagus* (12)	Conifers (18)
Hypnum cupressiforme var. filiforme	92·6	78·9	67·9	72·7	83·3	16·7
Eurhynchium myosuroides	80·2	44·7	57·2	31·8	75·0	27·8
Hypnum cupressiforme	60·5	84·2	75·0	100·0	83·3	88·9
Ulota crispa	40·7	78·9	17·9	63·6	33·3	—
Dicranum scoparium	25·9	5·3	42·9	—	—	—
Thuidium tamariscinum	24·7	21·0	14·3	—	—	—
Mnium hornum	17·3	10·5	39·6	9·1	25·0	16·7
Pylaisia polyantha	15·6	47·4	7·1	40·9	58·3	16·7
Camptothecium sericeum	12·4	39·5	7·1	59·0	8·3	5·6
Eurhynchium myurum	8·6	21·0	—	—	8·3	—
Mnium affine	6·2	5·3	3·6	—	—	11·1
Hylocomium splendens	5·0	—	—	—	—	—
H. loreum	3·7	—	—	—	—	—
Plagiothecium undulatum	3·7	—	—	—	—	—
Hylocomium brevirostre	2·5	7·9	—	—	—	
Brachythecium purum	2·5	—	—	—	—	—
B. rutabulum	1·2	7·9	—	9·1	8·3	11·1
Hypnum Schreberi	1·2	2·6	3·6	—	—	—
Polytrichum formosum	1·2	—	—	—	—	—
Dicranella heteromalla	—	—	—	—	—	5·6
Neckera complanata	—	5·3	—	—	—	—
Brachythecium salebrosum	—	5·3	—	—	—	—
Hylocomium triquetrum	—	2·6	—	—	—	—
H. squarrosum	—	2·6	—	—	—	—
Bryum sp.	—	2·6	—	—	—	—
Tetraphis pellucida	—	—	3·6	—	—	—

Autecology of the commoner mosses

It is worth while to consider individually some of the species present in highest frequency.

Eurhynchium myosuroides is the commonest constituent of the basal zone of trees, particularly if they are at all sheltered. Its frequency was highest upon the rough-barked trees, i.e. oaks and old birches, and fell rapidly with increasing exposure. For example it was found on only 47·4 % exposed oaks and 26·3 % exposed ashes. It was commonest on the splayed-out part of the trunk and was not often found upon the vertical part, particularly if *Hypnum cupressiforme* var. *filiforme* was present in any quantity. It rarely reached more than 1 ft. above the ground and was loosely attached, coming away easily in large masses.

Dicranum scoparium also showed intolerance of exposure. For example note the decrease in frequency with increase of exposure in oaks:

Sheltered	Open, *not* to west	Open, to west	Exposed
43·8%	30·4%	17·4%	15·8%

It is a ground moss and normally grows round the base of trees which are sheltered or in a position well supplied with moisture, but in Achnacloich it was frequently found in crotches of trees (birch in particular) some feet above the ground, if the tree was sheltered. Note in Table VIII the high percentage of *Dicranum* on *Betula*.

Hypnum cupressiforme is also a moss of the basal zone as a rule, usually occurring above *Eurhynchium myosuroides* and below *Hypnum cupressiforme* var. *filiforme* (see diagram of zonation, p. 85). This moss is rarely found on the vertical parts of the trunk, but is present on the splayed-out base and sometimes in crotches or on the uppermost side of a leaning tree. This seeming preference for a horizontal rather than a vertical position may be due to advantages resulting from a more adequate light supply. It would be very interesting to know what combination of factors, external and internal, produces a state of affairs in which the type of the species (*H. cupressiforme*) appears to be practically limited to the more horizontal parts of the trunk, while its variety *filiforme* is just as markedly found upon the vertical parts of the trunk.

Olsen (1916, 1917), however, says that mosses are usually found on the upper side of the inclined trunks of forest trees—being most abundant on slopes of over 10°—and scanty or lacking on perpendicular stems. He suggests that this is due to rain in a wood falling nearly vertically. In the Achnacloich district, which has a much heavier rainfall, this restriction does not hold good, and even vertical trees have a very heavy moss covering (see p. 85).

This species was found on nearly all the trees but never in such quantity as *Eurhynchium myosuroides*. It occurred most frequently on *Acer*, reaching 100% (see Table VIII) but at its lowest frequency gave a percentage of 60·5 (*Quercus*). Exposure caused a reduction in quantity but this reduction was not nearly so marked as in *Eurhynchium*.

Hypnum cupressiforme var. *filiforme* is one of the most frequent mosses, second only to *H. cupressiforme*. It usually forms a wide zone above *Eurhynchium* and its own type, and if the tree is at all sheltered and of reasonable age this variety may form a complete covering of the bark in conjunction with various lichens. This is particularly true of oaks. On exposed trees and young trees with smooth bark the moss covering is sparser and thinner, and *Hypnum cupressiforme* var. *filiforme* does not grow so high upon the tree. In fairly young oaks it often spreads upwards in the cracks of the bark, and spreads laterally from these cracks and downwards from the crotches. On sheltered trees it appears to overrun *Ulota*, which does not cover the bark rapidly but forms compact cushions, and on exposed, and on young, trees the *Hypnum*

cupressiforme var. *filiforme*, although somewhat reduced in quantity, is able to withstand a good deal of exposure, probably because it adheres closely to the bark.

Other less important mosses include *Mnium hornum* which grows round the bases of trunks and upon outspread roots reaching its highest values on birch and beech, and occurs for the most part in fairly sheltered situations except where crowded out by a very rank moss carpet. *Thuidium tamariscinum*, *Hylocomium* spp. and *Brachythecium* spp. are ground-carpet mosses and are only found round and upon the bases of sheltered trees which are usually zoned.

Three more mosses must be mentioned individually. They come into a different category, and behave more or less similarly. These are *Ulota crispa*, *Pylaisia polyantha* and *Camptothecium sericeum*. *Ulota* is an acrocarpous moss with a good attachment system and a compact habit. It forms clumps on trees whose bark is so smooth as to preclude the advent of most species. It is tolerant of exposure, probably because of its strong attachment, making it resistant to strong wind, associated with the capacity of its shoots to withstand drying for long periods without harm (Olsen, 1916, 1917). Thus it is found on 73·7 % exposed oaks, and on 78·9 % exposed ashes, showing a high degree of tolerance of exposure. On the other hand it is very intolerant of competition, occurring upon only 18·8 % sheltered oaks but 83·3 % sheltered ashes, showing that where the total moss covering (particularly *Hypnum cupressiforme* var. *filiforme*) is not so continuous *Ulota* manages to hold its own most successfully. Presumably this intolerance of competition is related to the fact that *Ulota* cannot spread over the bark vegetatively, whereas *Hypnum cupressiforme* can. *Ulota* is, however, a good colonizer, being nearly always in fruit it can spread rapidly from tree to tree; the number of tiny clumps on an individual young tree or exposed tree bearing ample witness to this fact.

Pylaisia polyantha is a fairly uncommon moss. It appears to be not very tolerant of exposure and quite as intolerant of competition as *Ulota*. Thus it is found on 31·6 % exposed oaks and 36·9 % exposed ashes, but on 58·3 % sheltered ashes and no sheltered oaks. Probably this moss which has prostrate, rooting shoots is easily overgrown by the ranker and more luxuriant *Hypnum cupressiforme* var. *filiforme*. *Pylaisia* is always rather slender and wispy in appearance, with a beautifully pinnate habit reminiscent of a young plant of *Camptothecium sericeum*, which indeed it closely resembles in the field. The tips of the shoots tend to curl slightly upwards and end in a tuft rather than a point of leaves.

Camptothecium sericeum does not appear to be a colonizer but somewhat resembles *Pylaisia* in habitat, although as a rule it grows on the base of the trunk. It can be quite a considerable constituent of the basal zone. It is more intolerant of exposure than *Pylaisia*, for example, it is found on only 5·3 % exposed oaks and 31·6 % exposed ashes, on 33·3 % sheltered ashes and no sheltered oaks.

The most important factor in determining the presence and the frequency of these three species is the comparative frequency of other mosses. Since they are capable of withstanding a certain amount of exposure they tend to show high frequencies on exposed trees, but the fact that they are also very frequent on young trees whose bark is still smooth and upon sheltered trees when for any reason the covering of other mosses is scanty shows that the amount of competition with which they have to contend is more important.

DIFFERENCES BETWEEN THE TREES IN RELATION TO THEIR EPIPHYTIC MOSS FLORA

One cannot study the autecology of the mosses, particularly the three species just dealt with, without perceiving that there is some difference between the moss floristic of different species of tree, for example of oaks and ashes. A useful comparison can therefore be made between the commonest mosses, and their frequencies, found upon the sheltered trees of oak, ash, birch, sycamore, etc., taking the sheltered trees only in order to eliminate the effects of exposure (Table IX).

Table IX. *Frequencies of the commonest mosses on sheltered trees*

Commonest mosses	*Quercus*	*Fraxinus*	*Betula*	*Acer*
Hypnum cupressiforme var. filiforme	100·0	91·6	90·0	90·0
Eurhynchium myosuroides	75·0	75·0	70·0	30·0
Hypnum cupressiforme	43·8	**100·0**	20·0	**100·0**
Ulota crispa	18·8	**83·3**	20·0	**60·0**
Dicranum scoparium	**43·8**	—	**80·0**	—
Thuidium tamariscinum	75·0	41·6	40·0	—
Pylaisia polyantha	—	**58·3**	—	**30·0**
Camptothecium sericeum	—	**33·3**	—	**50·0**
No. of trees studied	16	12	10	10

Figures in heavy type indicate comparable occurrences on the two members of the pairs *Quercus* and *Betula*, *Fraxinus* and *Acer*.

It will be seen from Table IX that the species considered may be taken in pairs, that *Quercus* and *Betula* appear to have a similar moss floristic, and also *Fraxinus* and *Acer*. *Hypnum cupressiforme* var. *filiforme*, however, appears to be uniformly successful on all sheltered trees, probably because it is very quick growing and is not affected to any great extent by the presence of other mosses. *Eurhynchium myosuroides* has an unaccountable drop to 30% on *Acer*. *Hypnum cupressiforme*, *Ulota crispa*, *Pylaisia polyantha* and *Camptothecium sericeum* all show markedly higher figures for *Fraxinus* and *Acer* than for *Quercus* and *Betula*. This difference is almost certainly due to differences in the nature of the bark. The oaks and birches have a rough bark. (The birches examined were old trees with fissured bark round the lower parts of the trunk, affording a very good situation for mosses.) Sycamore and ash on the other hand have a much smoother bark, even in very large trees, nor are these similarities to be attributed to the same habitats, e.g. all the sycamores came from one plantation, but the ashes came from various other situations. On the smoother bark of *Acer* and *Fraxinus* the species with good attachment,

such as *Ulota* and *Pylaisia*, are probably successful because the mosses which usually suppress them are not so efficient on smooth bark, e.g. *Hypnum cupressiforme* var. *filiforme*, which is found on practically all these trees but is very much sparser on ash than oak.

Dicranum scoparium has its highest frequencies on sheltered oaks and birches, but probably this needs much rougher bark. Since *Dicranum* and *Hypnum cupressiforme* are present on nearly half the sheltered oaks (both 43·8 %) it may be suggested that the presence of one precludes the presence of the other, especially as *Hypnum cupressiforme* is found on 100 % of ashes and sycamores and *Dicranum scoparium* is not found at all on these trees (see Table IX). Investigation, however, shows that on oaks, for example, out of 16 sheltered trees, 5 have no *Dicranum* or *Hypnum*, 4 have only *Dicranum*, 4 have only *Hypnum*, and 3 have both *Dicranum* and *Hypnum*. From this we may conclude that the presence of one does not prevent the other flourishing, and that the presence of *Dicranum* on *Quercus* and *Betula*, and its absence from *Acer* and *Fraxinus* must be due to bark differences, physical or chemical. In this case the physical difference of the rough bark of oak and birch contrasted with the comparatively smooth bark of sycamore and ash accounts for the difference in floristic. One instance was found in which the chemical differences of the bark were seen to be in operation. *Tetraphis pellucida* was found only on *Betula*, and du Rietz (1932) has shown that birch bark is very acid. Other observers have found that *Tetraphis* is markedly calcifuge, and Kessler (1914) has proved that *Tetraphis* spores cannot germinate in even slightly alkaline media.

No mosses which were frequent were at the same time specific to any tree—although *Tetraphis* was found occasionally on *Betula* and *Neckera complanata* was found on ash trees only—but marked differences between the trees appear to be due to the interacting factors of the environment, the physical nature of the bark, and the degree of tolerance exhibited towards competition by the moss species concerned. It must be borne in mind, however, that woods on different soils will in all probability have different moss ground floras, and hence different mosses will appear in the basal zones of the trees from the ground habitat. This factor should not affect the higher zones of the tree bark.

Summary

1. A comparative study was made of the moss flora on different species of trees, growing under different environmental conditions in Argyll.

2. This district offers a very favourable habitat for mosses owing to the prevailing climatic conditions—cool winds and heavy rainfall.

3. Although the mosses upon various species of trees were studied, special attention was paid to oaks, since they appear to form natural woodland in this neighbourhood and also because the moss floristic upon them is evidently affected by exposure.

4. On sheltered trees the moss and lichen covering was very heavy on trunk, branches, and even small twigs, and showed marked zonation.

5. As exposure to the prevailing winds increased the moss covering became scantier, its zoning much less marked, and the vertical extent of the zones much reduced.

6. The lowest zone on sheltered trees consisted of moss-carpet species, the middle zones of *Eurhynchium myosuroides*, *Hypnum cupressiforme* and *H. cupressiforme* var. *filiforme*, and the top zone of pioneer species such as *Ulota crispa* and *Pylaisia polyantha*.

7. A comparison of trees on which the mosses were zoned with those on which they were not showed that the mosses most commonly found on the latter were pioneer species, e.g. *Ulota* and *Pylaisia*.

8. A correlation of zonation with exposure showed that all sheltered trees were zoned, and that less than half the exposed trees were zoned.

9. The results obtained for ash and other trees, of which fewer individuals were examined confirmed those obtained for oak.

10. The moss covering of ash trees was not on the whole so dense as that on oaks. Pioneer species appeared in lower zones than on oaks.

11. Some study was made of the autecology of some of the most frequently encountered species.

12. A comparison was made of the commonest mosses growing on oak, ash, birch, and sycamore, and it was shown that the pairs oak and birch, ash and sycamore, behaved differently. The differences were accounted for chiefly by differences in the roughness of the bark, chemical differences playing only a very small part.

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THE MARINE ALGAL COMMUNITIES OF CASTLETOWN BAY, ISLE OF MAN

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(*With two Figures in the Text*)

Introduction

An intensive survey of an area on the Manx coast was carried out during the period December 1932 to November 1934 with the object of determining the composition, seasonal variation and zonation of the algal communities of the area. In the same district Knight & Parke (1931) had already made a syste-

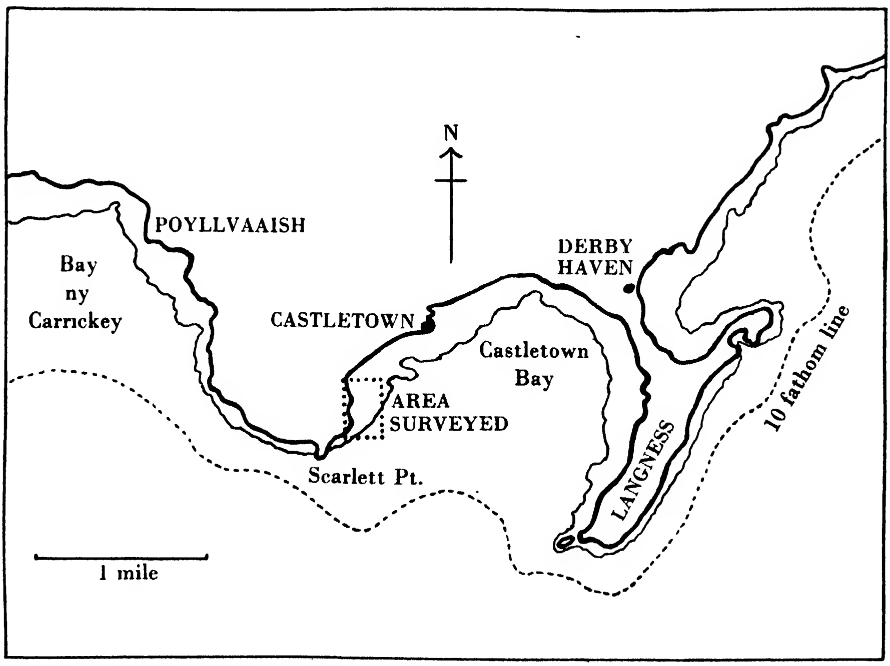

Fig. 1. Map of south-east corner of the Isle of Man, showing the position of the Survey Area.

matic survey of the algal flora and dealt with important biological problems, such as the duration of life of the species and algal migrations on the shore.

The area chosen for survey, about 18 acres in extent, is situated at the west side of Castletown Bay near Scarlett Point (Fig. 1). The southern portion

is rocky and consists of more or less parallel ledges of carboniferous limestone running in a north-east to south-west direction. These ledges tilt, sometimes quite steeply, in a west-north-west direction, i.e. they slope towards the land, so that pools form on the landward side of each terrace. The central portion of the area slopes more gently and the rock is in the form of irregular ledges which alternate with unbroken smooth stretches. The northern portion slopes very gently and includes considerable areas of sand, pebbles and boulders.

A detailed examination of the algal vegetation was made at a large number of scattered positions in the area and along two belt transects, each 60 ft. wide, extending from high water to low water of spring tides; one of these transects crosses the southern ledge formation and the other the central part of the area. A general study was made of all intervening portions of the area.

The tidal range at Castletown is considerable (18 ft. (5·5 m.) at ordinary spring tides) and since the slope is gradual, except at the extreme southern part, the intertidal zone is wide with a maximum of about 1500 ft. (457 m.) at spring tides. A map of the area, based on that of the Ordnance Survey, was made and tidal contours inserted (Fig. 2). I have to thank Mr J. R. Bruce for assistance in connexion with the necessary levelling. Levels were reduced from a bench mark 23·5 ft. (7·16 m.) above Ordnance Datum, i.e. mean sea-level at Douglas, I.O.M., and recorded to the nearest $\frac{1}{10}$ foot.

PHYSICAL CONDITIONS

The prevailing wind (from 10 years' records at the Marine Biological Station, Port Erin) is westerly except in spring when it is south-east. Strong winds are common chiefly from the north-west and west in winter, south-east in spring and west, north-west, north and south-east in autumn. The southern part of the area is most exposed, while the rest of the area lying farther inside Castletown Bay is exposed only to south and south-east winds. Owing to the ledge structure and the greater wind exposure the splash zone is considerable on the exposed southern portion and influences the range of algal vegetation: in the bay the splash zone is negligible.

Sea temperature at Port Erin (Bruce, 1928) varies from a mean maximum of about 13·8° C. in August to a mean minimum of about 6·8° C. in March. The mean temperature of the air is highest (about 14·8° C.) in July and lowest (5·3° C.) in February. Sea and air have about the same mean temperature in April (7·5° C.) and September (13·7° C.).

Variations in light intensity must influence algal vegetation considerably. No measurements were made of light intensity but the sunshine records taken at King William's College, near Castletown, show considerable variation from year to year in the same month. A change in the average light intensity probably results in an acceleration or retardation of rate of influx of annual species and may also cause earlier or later reproduction.

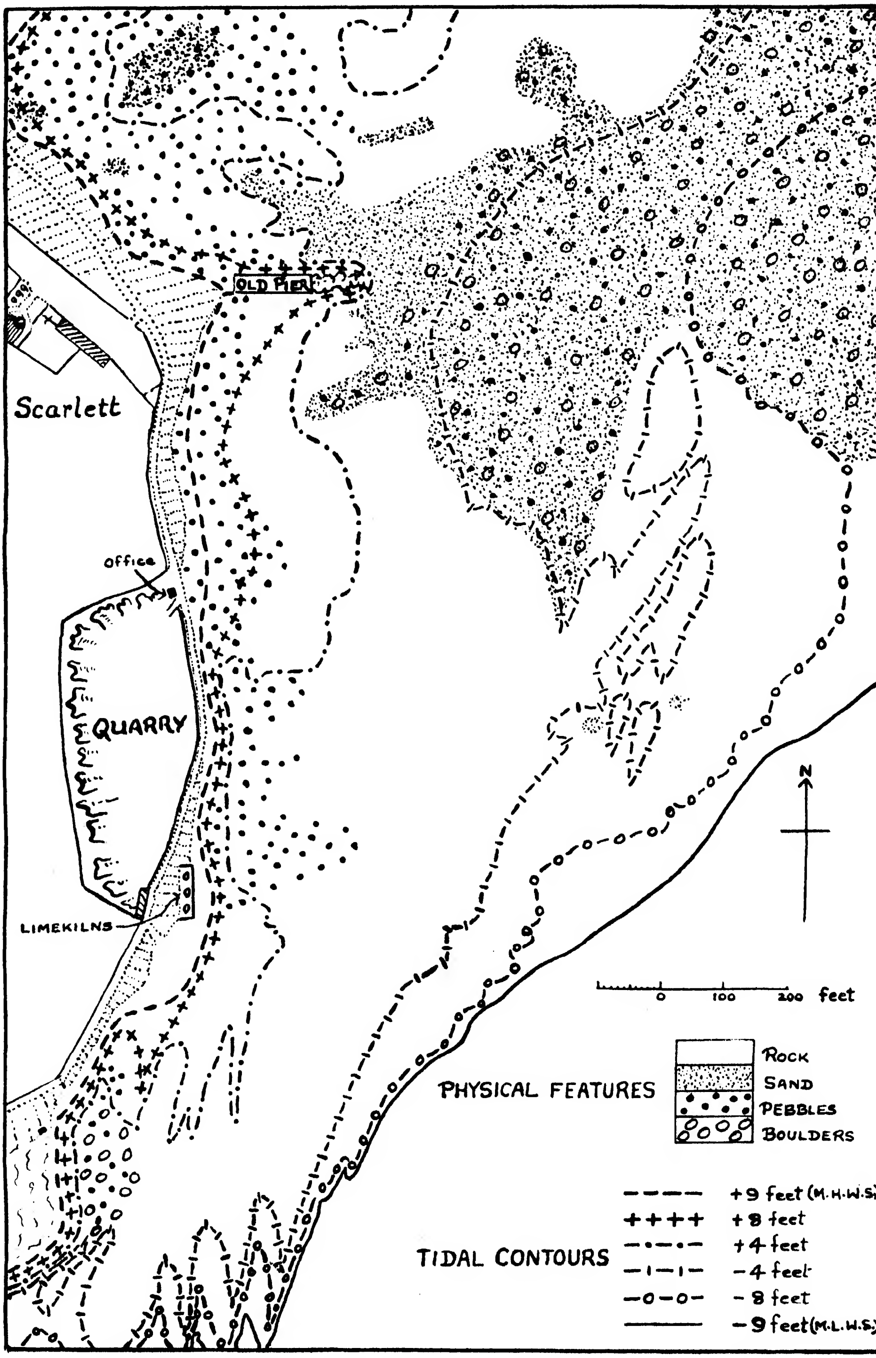

FIG. 2. Map of Survey Area on west side of Castletown Bay, Isle of Man.

The southern and central parts of the area are not appreciably influenced by land drainage and there is no perceptible effect on the algal vegetation. In the northern portion, however, a small stream enters and along its course Chlorophyceae are conspicuous.

TIDES AND CURRENTS

The Isle of Man tides originate in the Atlantic Ocean, west of Ireland. The tidal wave enters the Irish Sea partly through the North Channel and partly through St George's Channel, the two components meeting just south of the Isle of Man. In the Castletown area the flood tide makes in a north-east direction parallel with the coast, and the ebb tide flows past Langness Point in a south-west direction but sets up an eastward eddy round Castletown Bay.

High water at full and change of the moon is 11 hr. 10 min., thus low water of spring tides occurs in the early morning and in the evening. This is of importance to the vegetation of the lowest levels because it is never exposed to strong sunlight when uncovered.

A mean tidal range-line of 14 ft. (4·24 m.) strikes the Isle of Man at Castletown (Admiralty Chart No. 301, 1931) giving a mean range of 18 ft. (5·5 m.) at spring and 10 ft. (3·04 m.) at neap tides. Levels throughout this paper are given in feet above (+) or below (−) M.S.L. The tidal levels for Castletown are as follows:

Mean high-water springs (M.H.W.S.)	+9 ft.
Mean high-water neaps (M.H.W.N.)	+5 ,,
Mean sea-level (M.S.L.)	0 ,,
Mean low-water neaps (M.L.W.N.)	−5 ,,
Mean low-water springs (M.L.W.S.)	−9 ,,

THE CHIEF ALGAL COMMUNITIES OF THE AREA

Since the factors determining the composition and distribution of marine algal communities have not yet been satisfactorily analysed it is undesirable to use the term "association" for such communities, for at present it is uncertain whether the algal communities which have been called associations are in any way equivalent to those communities to which that term has been applied on land. It seems advisable, therefore, to use the more comprehensive term "community" although many of the communities described in this paper are similar to those which have been called associations by Cotton (1912), Rees (1935), Grubb (1936) and others. While the chief communities seem to be determined mainly by physical conditions, their general facies is subject to considerable variation, since many algae appear only at certain seasons of the year and of these some are short-lived. In the present survey considerable attention has been paid to the seasonal range of species. Many of the data

obtained are presented in the following pages in tabular form rather than in long and detailed descriptions of the communities.

The chief communities recognized at Castletown Bay are as follows:

I. *Communities of rocky shores*

A. *Porphyra-Urospora-Ulothrix* community.
B. *Pelvetia-Fucus spiralis* community.
C. *Ascophyllum* community.
D. *Fucus vesiculosus* community.
E. *Laurencia-Lomentaria* community.
F. *Laurencia-Cladophora-Rhodochorton* community.
G. *Fucus serratus* community.
H. *Himanthalia* community.
J. *Enteromorpha-Cladophora-Chordaria* community.
K. *Laminaria* community.
L. Community hanging under ledges.
M. Pool vegetation.

II. *Communities of sand and pebbles*

N. *Enteromorpha* community.
O. Sand-pool vegetation.
P. Sublittoral community on pebbles.

Of the twelve communities which characterize the rocky shore A, B, C, D, E and F belong to the littoral region as defined by Cotton (1912), i.e. extending from the level of highest marine vegetation to the level of low-water mark at neap tides; the communities J and K belong to the sublittoral region which begins at the lower limit of the littoral region and extends downwards to the limit of algal vegetation; G, H, L and M occur in both littoral and sublittoral regions. Of the three communities developed on sand or pebbles, the first is littoral and the third sublittoral, while sand-pool vegetation occurs in both regions.

I. Communities of rocky shores

A. *Porphyra-Urospora-Ulothrix* community

This community is best developed on the highest parts of the exposed rocky shore towards the south and is practically absent from the sheltered northern portion of the area. It occupies a zone of relatively smooth undulating rock surface between +4 and +8 ft., lying just above the barnacle zone. Relatively few species enter into the composition of this community. They are *Oscillatoria* spp., *Calothrix scopulorum*, *Prasiola stipitata*, *Ulothrix flacca*, *Urospora isogona*, and *Porphyra umbilicalis* var. *linearis*. The community occurs seasonally. The three co-dominant species *Porphyra umbilicalis* var.

linearis, *Urospora isogona* and *Ulothrix flacca* begin to appear in November and December, reaching their maximum growth and development in March of the following year and disappear in early summer. *Prasiola* does not appear until January but by March it is abundant and is co-dominant with *Porphyra*, *Urospora* and *Ulothrix*. A thin layer of mud which accumulates in the hollows of the undulating rock surface seems favourable for the development of blue-green algae of which *Oscillatoria* and *Calothrix* are abundant and persistent. *Porphyra umbilicalis* var. *laciniata* is the only other species which persists throughout the year.

A marked zonation is evident among the members of the community, *Urospora* occupying the highest levels followed by *Porphyra* (var. *linearis*) and *Prasiola*, while *Ulothrix* and *Porphyra* (var. *laciniata*) occur only at the lowest limit of the zone.

Although this community has not hitherto been described for the British coasts it agrees closely with the "*Bangia-Urospora* society" described by Rees (1935) for south-west Ireland. The most significant differences are the absence of *Prasiola* and the inclusion of *Bangia fusco-purpurea* in the Irish community. Although *Bangia* occurs at Castletown it is found at lower levels on the shore and is usually a pure growth.

B. *Pelvetia-Fucus spiralis* community

This community is well developed on the northern and central parts of the area ranging from +5 to +7·4 ft. but is practically absent on the southern portion, where isolated plants are present only in cracks and crevices of the ledges. This locally poor development is probably due to the smooth surface of the rock, for the rock in the other parts of the area is much more broken and offers a better anchorage for the plants. *Pelvetia* and *Fucus spiralis* occupy two fairly clearly defined zones, the former ranging higher, but they are treated together because of similarities in degree of development in relation to physical conditions and in the accompanying flora; the latter consists of only two species, *Rivularia atra* and *Catenella repens*.

C. *Ascophyllum* community

This community shows much variation within the survey area. *Ascophyllum* is poorly developed on the southern portion, the plants being stunted and carrying a heavy parasitic growth of *Polysiphonia fastigiata*. Its vertical range here is small (from +1 to +3·3 ft.) and its distribution discontinuous because of the ledges. Towards the north, the size and development of the plant quickly improves. Just south of the old pier (see Fig. 2) at the edge of the sandy bay, the growth is dense and the plants are from 2 to 3 ft. long. Here it occurs on rock and boulders at levels from +2·7 to +4·1 ft. There is very little parasitic growth of *P. fastigiata* but in spring and summer the epiphyte *Pylaiella littoralis* is common. Numerous small algae are associated

with *Ascophyllum* forming an undergrowth, which is entirely hidden by the dominant species in the northern part of the area. Here the uniformity of shade maintains a more or less constant undergrowth throughout the year, of which the commonest species are *Cladophora rupestris*, *Cladostephus spongiosus*, *Gelidium crinale* var. *genuinum*, *Chondrus crispus*, *Delesseria alata*, *Lomentaria articulata*, *Laurencia pinnatifida*, *Plumaria elegans*, *Lithothamnion Lenormandi* and *Corallina officinalis*. On the ledges towards the south, where *Ascophyllum* is sparser, the undergrowth is much more varied and many additional species, several annual and seasonal, are included.

The relative abundance and seasonal occurrence of the species forming the *Ascophyllum* community are shown in Table I.

The symbols used in the tables are as follows: d. = dominant, cd. = co-dominant, a. = abundant, f. = frequent, o. = occasional, l. = locally.

Table I. *Species forming the* Ascophyllum *community*

Species	Sp.	S.	A.	W.
Ascophyllum nodosum Le Jol.	d.	d.	d.	d.
Callithamnion Hookeri Ag.	o.	—	—	o.
Ceramium rubrum Ag.	o.	o.	o.	o.
Chondrus crispus Stackh.	f.	f.	f.	f.
Cladophora albida Kütz.	—	f.	—	—
C. flexuosa Harv.	f.	—	—	o.
C. rupestris Kütz.	a.	a.	a.	a.
Cladostephus spongiosus Ag.	f.	f.	f.	f.
Corallina officinalis L.	o.	o.	o.	o.
Delesseria alata Lamour.	f.	f.	f.	f.
Enteromorpha clathrata J. Ag. var. genuina Batt.	f.	—	f.	o.
Gelidium corneum Lamour.	f.	f.	f.	f.
G. crinale J. Ag. var. genuinum Hauck	a.	a.	a.	a.
Hildenbrandtia prototypus Nardo var. rosea Kütz.	o.	o.	o.	o.
Laurencia hybrida Lenor.	f.	—	o.	f.
L. pinnatifida Lamour.	a.	f.	a.	a.
Leathesia difformis Aresch.	—	f.	o.	—
Lithothamnion Lenormandi Fosl.	f.	f.	f.	f.
Lomentaria articulata Lyngb.	f.	f.	f.	f.
Monostroma Grevillei Wittr.	f.	—	—	—
Plumaria elegans Schm.	f.	f.	f.	f.
Polysiphonia fastigiata Grev.	l.a.	l.a.	l.a.	l.a.
P. nigrescens Grev.	f.	o.	f.	o.
Pylaiella littoralis Kjellm.	f.	f.	—	—
Ulva lactuca L. var. latissima DC.	f.	f.	f.	f.

D. *Fucus vesiculosus* community

Several areas dominated by *Fucus vesiculosus* occur on barnacle-covered rock below the level of *Ascophyllum* on the ledges at the extreme southern part of the area; these range from -3 to $+1$ ft. The undergrowth is sparse and usually consists of a scattered growth of *Laurencia pinnatifida*, *Lithothamnion Lenormandi*, *Corallina officinalis* and a few seasonal species, e.g. *Cladophora albida*, *Leathesia difformis* and *Polysiphonia fibrata*. Common epiphytes on *Fucus vesiculosus* are *Enteromorpha compressa*, *Urospora bangioides*, *Pylaiella littoralis* and *Elachistea fucicola*.

In the extreme northern sheltered part of the area, a fairly dense growth of *Fucus vesiculosus* occurs at a much higher level (between +4·1 and +4·9 ft.) just above the dense *Ascophyllum* zone, although a scattered growth occurs much lower down the shore on boulders in the sandy bay. The individual plants of *Fucus vesiculosus* are better developed here and the undergrowth is similar in composition to that underlying the *Ascophyllum* in the zone just below

E. *Laurencia-Lomentaria* community

This distinctive community dominated by *Laurencia pinnatifida* and *Lomentaria articulata* occurs only on the ledges at the extreme southern portion of the area between +0·5 and −1·8 ft. As the slope of the ledges where it occurs is gradual the community covers a considerable area. Much of the substratum of rough and pitted limestone is covered by *Lithothamnion* to which are attached several of the species, e.g. stunted *Corallina officinalis*, *Laurencia pinnatifida*, *Cladophora rupestris* and *Cladostephus spongiosus*. These bear numerous epiphytic species, e.g. *Lomentaria articulata*, *Gelidium corneum*, *Ceramium rubrum*, *C. strictum* and *Enteromorpha clathrata*. Much of the vegetation is interwoven, giving lodgement to a quantity of sandy mud. The composition and the appearance of the vegetation are constantly changing throughout the year as many of the species are seasonal and short-lived. A measure of the extent of seasonal change in the community at the level of −1·5 ft. was obtained by finding the volume of each species growing on 0·25 sq. m. of rock surface at intervals of 2 months from May 1933 to March 1934. The area selected was scraped clean, the species separated and their volume measured by displacement. The results are shown in Table II, excluding *Lithothamnion* and the sparse plants of *Fucus serratus* and *Himanthalia*. The largest number of species was present in May when 17 of the 20 species occurred, and the fewest in January when only 11 were found. The quantity of vegetation, however, was greatest in March and least in September. Of the co-dominants *Laurencia* is, on the whole, more abundant than *Lomentaria*, but the two species are to a large extent complementary in their occurrence, *Laurencia* being most abundant in November while *Lomentaria* reaches its maximum in May.

The general appearance of the community is decided largely by the seasonal epiphytic species which mask to a great extent the underlying vegetation. In winter, when epiphytes are few *Laurencia* is conspicuous; in spring *Lomentaria*, which is chiefly epiphytic, practically covers the other vegetation, while in summer the epiphytes *Ceramium rubrum* and *Enteromorpha clathrata* overlie much of the other vegetation.

Although *Laurencia* is most abundant when associated with the above species, it continues to be prominent in two communities which occur below this level, viz. the *Laurencia-Cladophora-Rhodochorton* community and the *Himanthalia* community. The *Laurencia-Lomentaria* community is similar to

the "*Laurencia-Gelidium* association" described by Rees (1935) for sheltered rocky coasts in south-west Ireland, where *Lomentaria* appears to be only frequent or locally dominant.

Table II. *Species of the* Laurencia-Lomentaria *community, showing the change in volume throughout a year*

	Volume in c.c. per sq. m.					
	1933				1934	
Species	May	July	Sept.	Nov.	Jan.	Mar.
Callithamnion Hookeri Ag.	12·8	0·8	1·6	0·8	2·4	8·0
Ceramium ciliatum Ducluz.	10·7	Trace	2·0	—	—	—
C. flabelligerum J. Ag.	—	—	—	—	Trace	27·2
C. rubrum Ag.	34·4	72·0	56·8	0·8	—	6·4
C. strictum Harv.	8·6	4·0	16·4	Trace	Trace	Trace
Chaetomorpha tortuosa Kütz.	1·1	7·2	1·2	Trace	Trace	—
Cladophora albida Kütz.	—	8·0	—	—	—	—
C. arcta Kütz.	32·2	—	—	—	—	—
C. rupestris Kütz.	5·4	28·0	8·4	10·4	128·0	32·0
C. utriculosa Kütz.	16·1	12·0	4·4	9·6	Trace	3·2
Cladostephus spongiosus Ag.	1·1	4·0	1·2	—	11·2	5·8
Corallina officinalis L.	194·0	108·0	124·2	108·0	313·6	180·0
Enteromorpha clathrata J. Ag. var. genuina Batt.	6·4	68·0	60·0	9·2	—	2·0
Gelidium corneum Lamour.	32·2	33·2	17·6	80·4	80·0	68·8
Laurencia pinnatifida Lamour.	644·4	372·0	468·0	1120·0	944·0	800·0
Leathesia difformis Aresch.	—	52·0	2·4	—	—	—
Lomentaria articulata Lyngb.	1288·8	264·0	27·2	161·6	372·8	1240·0
Monostroma Grevillei Wittr.	16·1	—	—	—	—	Trace
Porphyra leucosticta Thur.	2·1	—	—	—	—	1·2
Ulva lactuca L. var. latissima DC.	1·1	0·8	0·8	0·8	—	Trace
Total volume	2307·5	1034·0	792·2	1501·6	1852·0	2374·6
Total no. of species: 20	17	16	15	12	11	15

F. *Laurencia-Cladophora-Rhodochorton* community

This association is developed on rocks covered by sandy mud between 0 and −5 ft. in different parts of the area and is confined to this type of substratum. The vegetation is short and dense and a large number of species are included in the community (Table III). *Laurencia pinnatifida*, *Cladophora rupestris* and *Rhodochorton Rothii* are the most abundant but the dominance of each is irregular owing to variations in the thickness of the layer of sandy mud, the last mentioned occurring where the mud is thickest. Much of the vegetation is epiphytic, mainly on *Cladophora rupestris*, *Cladostephus spongiosus* and *Corallina officinalis*. Many of the species occur seasonally and of these *Leathesia difformis* is so abundant in summer as to become co-dominant. Most of the seasonal species, however, are patchy in their distribution and form small seasonal societies within the community. Table III shows the seasonal occurrence and abundance of the species composing the community.

This community is really a modification of the *Laurencia-Lomentaria* community owing to the accumulation of more sandy mud on the rock surface. It is similar to the "general association of sandy mud-covered rocks" described

Table III. *Species forming the* Laurencia-Cladophora-Rhodochorton *community*

Species	Sp.	S.	A.	W.
Acrochaetium virgatulum J. Ag.	o.	—	—	—
Callithamnion arbuscula Lyngb.	f.	—	f.	o.
C. brachiatum Bonnem.	—	—	—	o.
C. Hookeri Ag.	f.	f.	f.	f.
Ceramium ciliatum Ducluz.	a.	f.	o.	o.
C. rubrum Ag.	f.	f.	f.	f.
Chaetomorpha tortuosa Kütz.	a.	a.	o.	o.
Chondrus crispus Stackh.	f.	f.	f.	f.
Chylocladia ovata Batt.	f.	—	—	o.
Cladophora arcta Kütz.	f.	f.	—	—
C. flexuosa Harv.	f.	f.	—	o.
C. rupestris Kütz.	l.d.	l.d.	l.d.	l.d.
C. utriculosa Kütz.	—	o.	o.	—
Cladostephus spongiosus Ag.	f.	f.	f.	f.
Codium tomentosum Stackh.	—	—	o.	—
Corallina officinalis L.	f.	f.	f.	f.
Dasya arbuscula Ag.	—	—	o.	f.
Ectocarpus fasciculatus Harv. var. refracta Ardissone	o.	—	—	—
E. fasciculatus Harv. var. typica	—	—	o.	—
E. velutinus Kütz.	—	—	o.	—
Elachistea scutulata Duby.	—	—	o.	—
Fucus serratus L.	o.	o.	o.	o.
Gelidium corneum Lamour.	f.	f.	f.	f.
G. crinale J. Ag. var. genuinum Hauck	o.	o.	o.	o.
Griffithsia flosculosa Batt.	—	o.	—	—
Himanthalia lorea Lyngb.	o.	o.	o.	o.
Isthmoplea sphaerophora Kjellm.	f.	—	—	—
Laurencia pinnatifida Lamour.	l.d.	l.d.	l.d.	l.d.
Leathesia difformis Aresch.	—	cd.	—	—
Lomentaria articulata Lyngb.	f.	f.	f.	f.
Monostroma Grevillei Wittr.	f.	—	—	—
Polysiphonia fibrata Harv.	f.	o.	—	o.
P. spinulosa Grev.	—	—	—	o.
Porphyra leucosticta Thur.	f.	—	—	—
Pterosiphonia thuyoides Schm.	f.	f.	f.	f.
Rhodochorton Rothii Näg.	l.d.	l.d.	l.d.	l.d.
Rhodymenia palmata Grev. var. typica Batt.	o.	—	—	—
Sphacelaria cirrhosa Ag. var. fusca Holm. et Batt.	—	o.	o.	o.
Ulva lactuca L. var. latissima DC.	f.	—	—	—
Total no. of species: 39	28	23	24	24

by Rees (1935), although it differs somewhat floristically. It has also many resemblances to the "*Corallina-Cladostephus* community" of Cotton (1912), although in that community *Cladophora rupestris* and *Laurencia* are not noted.

G. *Fucus serratus* community

Fucus serratus occurs throughout the area forming a conspicuous zone near low-water mark. Towards the south, the densest growth occurs on the seaward sides of the gently sloping surfaces of the ledges between −4 and −2·2 ft. A sparser growth occurs between this and the upper limit of the *Laminaria* zone (−8 ft.). In the central part of the area the growth is even more luxuriant on the very gently sloping and broken-up ledges where it is dense right down to the *Laminaria* community. In the northern part it occurs in quantity on boulders and small areas of rock in the sandy bay. The commonest epiphytes

on *Fucus serratus* are *Ectocarpus tomentosus*, *Pylaiella littoralis*, *Elachistea fucicola* and *Rhodymenia palmata* var. *marginifera*. Many of the species which form the undergrowth in the community are the same as those of the undergrowth in the dense *Ascophyllum* zone. It would appear that the shade condition prevailing under a dense growth of *Ascophyllum* and under *Fucus serratus* at a rather lower level is the determining factor in the occurrence of the prevalent species. Their seasonal occurrence and abundance in this community are shown in Table IV.

Table IV. *Species forming the undergrowth of the* Fucus serratus *community*

Species	Sp.	S.	A.	W.
Callithamnion Hookeri Ag.	o.	—	f.	f.
Ceramium rubrum Ag.	f.	f.	f.	f.
Chondrus crispus Stackh.	f.	f.	f.	f.
Cladophora albida Kütz.	—	o.	—	—
C. flexuosa Harv.	f.	—	—	—
C. rupestris Kütz.	a.	a.	a.	a.
Cladostephus spongiosus Ag.	f.	f.	f.	f.
Corallina officinalis L.	f.	f.	f.	f.
Delesseria alata Lamour.	f.	f.	f.	f.
Gelidium corneum Lamour.	f.	f.	f.	f.
G. crinale J. Ag. var. genuinum Hauck	o.	o.	o.	o.
Gigartina stellata Batt.	f.	f.	f.	f.
Isthmoplea sphaerophora Kjellm.	f.	—	—	—
Laurencia pinnatifida Lamour.	o.	o.	o.	o.
Lithothamnion Lenormandi Fosl.	o.	o.	o.	o.
L. polymorphum Aresch.	a.	a.	a.	a.
Lomentaria articulata Lyngb.	f.	f.	f.	f.
Monostroma Grevillei Wittr.	f.	—	—	—
Plumaria elegans Schm.	f.	f.	f.	f.
Polysiphonia nigrescens Grev.	o.	o.	o.	o.
P. urceolata Grev. var. typica J. Ag.	f.	f.	o.	o.
Porphyra leucosticta Thur.	f.	—	—	—
Ulva lactuca L. var. latissima DC.	o.	o.	o.	o.

H. *Himanthalia* community

An abundant growth of *Himanthalia* occurs on the ledges towards the south of the area but not a single plant was found in either the central or northern parts. On the ledges it replaces the lower part of the *Fucus serratus* zone and continues down to the *Laminaria* association, i.e. it occupies a zone between -4 and -8 ft. and therefore belongs mainly to the sublittoral region. The vertical range of *Himanthalia* is somewhat wider but it is dominant only between these levels. Its occurrence only on the ledges is, no doubt, related to the more turbulent condition of the water there; Børgesen (1905), Cotton (1912) and Rees (1935) also found it to be a surf-loving species. Scattered plants of *Fucus serratus*, *Alaria esculenta* and *Laminaria digitata* are mixed with *Himanthalia* on the ledges, and underneath there is a short dense undergrowth consisting largely of the calcareous species *Lithothamnion polymorphum*, *L. lichenoides* and *Corallina officinalis*. Other conspicuous algae of the undergrowth are *Laurencia pinnatifida*, *Chylocladia ovata* and *Porphyra leucosticta* in spring; *Leathesia difformis* in summer and *Dasya arbuscula* in autumn.

Epiphytes on *Himanthalia* are numerous and occur on the underside of the vegetative "buttons" as well as on the mature receptacles. Those on the vegetative thallus are representative of various species found in the undergrowth, but those on the receptacles do not belong to the undergrowth and are constant and characteristic, viz. *Ectocarpus velutinus*, *E. fasciculatus* and *Elachistea scutulata*.

Table V (p. 108) shows the seasonal occurrence and abundance of the species occurring as undergrowth in the *Himanthalia* community.

J. *Enteromorpha-Cladophora-Chordaria* community

This is a well-marked sublittoral community occurring on the ledges in spring and summer. It is best developed at the base of vertical ledge faces at the south of the area and is usually associated with some sandy mud on the rock surface. It has a small range, being restricted to a zone from about −5 to −6 ft. In spring the co-dominants are *Enteromorpha Linza* var. *lanceolata*, *Cladophora arcta* and *Chordaria flagelliformis*. Other abundant spring forms are *Scytosiphon lomentarius*, *Pylaiella littoralis* and *Dumontia incrassata*. In summer *Chordaria* is still dominant, *Cladophora arcta* is not nearly so abundant and *Enteromorpha Linza* has disappeared. *Dictyosiphon foeniculaceus* (epiphytic on *Chordaria*) and *Cystoclonium purpureum* are then the most conspicuous species along with *Chordaria*. Table VI (p. 109) gives a list of the species in the community and shows their relative abundance in spring and summer; the associated perennial species such as *Alaria esculenta*, *Chondrus crispus*, *Cladophora rupestris*, *Corallina officinalis* and *Fucus serratus* occur occasionally and represent only a small proportion of the vegetation.

There is no previous description of this community for the British Isles. The floristic composition of the community, however, is similar to that of Børgesen's (1905) "*Stictyosiphon* association" of sheltered coasts in the Faeröes, but the latter occurs chiefly on a substratum of pebbles and in more sheltered places than at Castletown.

K. *Laminaria* community

The Castletown area has a well-developed *Laminaria* community which is clearly divisible into two zones. The upper zone, where *L. digitata* is dominant, ranges from −8 to −10 ft.; the zone below dominated by *L. Cloustoni* is only visible at very low ebbs when the upper parts of the plants alone are exposed.

On the ledges towards the south *L. digitata* forms a continuous dense belt covering the rock surface and here some *Alaria esculenta* and *Himanthalia* occur along with it. At the north, *Laminaria digitata* occurs with much *L. saccharina* on the boulders throughout the sandy bay. Several common epiphytes which occur on *L. digitata* are *Ectocarpus fasciculatus*, *Rhodymenia palmata* var. *marginifera*, *Polysiphonia urceolata* and *Dermatolithon macrocarpum* var. *Laminariae* (on holdfast).

Table V. *Species forming the undergrowth of the* Himanthalia *community*

Species	Sp.	S.	A.	W.
Acrochaetium Daviesii Näg.	—	—	o.	—
A. virgatulum J. Ag.	o.	o.	o.	—
A. virgatulum J. Ag. var. luxurians Rosenv.	o.	o.	o.	—
Callithamnion arbuscula Lyngb.	—	o.	f.	—
C. brachiatum Bonnem.	—	—	—	o.
C. Hookeri Ag.	o.	o.	f.	f.
C. tetragonum Ag.	—	—	o.	—
Callophyllis laciniata Kütz.	—	—	—	o.
Ceramium echinotum J. Ag.	—	o.	—	—
C. rubrum Ag.	o.	f.	o.	o.
C. strictum Harv.	—	o.	—	—
Chaetomorpha tortuosa Kütz.	—	o.	—	—
Chondrus crispus Stackh.	f.	f.	f.	f.
Chylocladia ovata Batt.	a.	f.	o.	f.
Cladophora albida Kütz. var. refracta Thur.	—	o.	—	—
C. arcta Kütz.	f.	o.	—	—
C. Hutchinsiae Harv.	—	—	o.	—
C. lanosa Kütz.	o.	—	—	—
C. rupestris Kütz.	f.	f.	f.	f.
C. utriculosa Kütz.	—	f.	f.	—
Cladostephus spongiosus Ag.	f.	f.	f.	f.
Codium adhaerens Ag.	o.	o.	o.	o.
C. tomentosum Stackh.	o.	o.	o.	o.
Corallina officinalis L.	a.	a.	a.	a.
Corynophloea crispa Harv.	—	o.	—	—
Dasya arbuscula Ag.	—	—	a.	o.
Delesseria alata Lamour.	f.	—	—	—
Dermocarpa prasina Born.	o.	—	o.	o.
Desmarestia viridis Lamour.	o.	—	—	—
Dumontia incrassata Lamour.	f.	—	—	—
Ectocarpus simplex Crn.	o.	—	o.	—
Eudesme virescens (Carm.) J. Ag.	—	o.	—	—
Euthora cristata J. Ag.	—	—	o.	—
Gelidium corneum Lamour.	f.	f.	f.	f.
G. latifolium Born.	f.	f.	f.	f.
Gigartina stellata Batt.	f.	o.	o.	f.
Griffithsia flosculosa Batt.	f.	o.	f.	f.
Halurus equisetifolius Kütz.	—	—	o.	o.
Heterosiphonia plumosa Batt.	—	—	—	o.
Isthmoplea sphaerophora Kjellm.	o.	—	—	—
Laurencia pinnatifida Lamour.	f.	f.	f.	f.
Leathesia difformis Aresch.	o.	a.	—	—
Lithothamnion lichenoides Fosl.	f.	f.	f.	f.
L. polymorphum Aresch.	f.	f.	f.	f.
Lomentaria articulata Lyngb.	f.	o.	f.	f.
Melobesia minutula Fosl.	f.	f.	f.	f.
Monostroma Grevillei Wittr.	f.	—	—	—
Myrionema strangulans Grev. var. typica Batt.	—	f.	—	—
Nemalion multifidum J. Ag.	—	o.	—	—
Nitophyllum ramosum Batt.	f.	—	o.	o.
Phloeospora brachiata Born.	o.	—	—	—
Plumaria elegans Schm.	f.	f.	f.	f.
Polysiphonia Brodiaei Grev. var. typica Holm. et Batt.	o.	—	—	o.
P. fibrillosa Grev.	—	f.	—	—
P. nigrescens Grev.	f.	—	—	—
P. urceolata Grev. var. typica J. Ag.	o.	—	—	—
Porphyra leucosticta Thur.	a.	—	—	—
Pterosiphonia thuyoides Schm.	f.	f.	o.	o.
Rhodochorton Rothii Näg.	o.	o.	o.	o.
Rhodymenia palmata Grev. var. marginifera Harv.	f.	f.	f.	o.
R. palmata Grev. var. typica Batt.	f.	f.	f.	f.
Sphacelaria cirrhosa Ag. var. fusca Holm. et Batt.	—	o.	—	o.
Ulva lactuca L. var. latissima DC.	o.	—	—	—
Total no. of species: 63	42	39	36	32

Table VI. *The species forming the* Enteromorpha-Cladophora-Chordaria *community*

Species	Spring	Summer
Alaria esculenta Grev.	o.	o.
Asperococcus fistulosus Hook.	—	o.
Callithamnion arbuscula Lyngb.	o.	—
C. Hookeri Ag.	f.	f.
Ceramium ciliatum Ducluz.	o.	o.
C. echinotum J. Ag.	—	o.
C. rubrum Ag.	f.	f.
C. strictum Harv.	—	o.
Chondrus crispus Stackh.	o.	o.
Chordaria flagelliformis Ag.	cd.	d.
Cladophora albida Kütz.	—	f.
C. arcta Kütz.	cd.	f.
C. flexuosa Harv.	o.	—
C. lanosa Kütz.	o.	—
C. rupestris Kütz.	o.	o.
C. utriculosa Kütz.	o.	o.
Cladostephus spongiosus Ag.	f.	f.
Codium tomentosum Stackh.	o.	o.
Corallina officinalis L.	o.	o.
Cystoclonium purpureum Batt.	o.	a.
Dictyosiphon foeniculaceus Grev.	—	a.
Dumontia incrassata Lamour.	a.	—
Ectocarpus confervoides Le Jol.	f.	—
Enteromorpha compressa Grev.	f.	f.
E. Linza J. Ag. var. lanceolata (Kütz.)	cd.	—
Eudesme virescens (Carm.) J. Ag.	—	o.
Fucus serratus L.	o.	o.
Laminaria saccharina Lamour.	o.	o.
Laurencia pinnatifida Lamour.	o.	o.
Leathesia difformis Aresch.	—	f.
Lithophyllum incrustans Fosl.	o.	o.
Litosiphon Laminariae Harv.	—	o.
Myrionema strangulans Grev. var. typica Batt.	—	f.
Myriotrichia clavaeformis Harv.	—	f.
M. filiformis Harv.	—	f.
Phloeospora brachiata Born.	—	o.
Polysiphonia Brodiaei Grev. var. typica Holm. et Batt.	o.	—
P. fibrata Harv.	o.	o.
P. urceolata Grev. var. typica J. Ag.	o.	—
Porphyra leucosticta Thur.	f.	—
Punctaria latifolia Grev. var. genuina Batt.	—	o.
P. plantaginea Grev.	f.	—
Pylaiella littoralis Kjellm.	a.	—
Rhodochorton Rothii Näg.	o.	o.
Rhodomela subfusca Ag.	o.	o.
Rhodymenia palmata Grev. var. typica Batt.	f.	f.
Scytosiphon lomentarius J. Ag.	a.	f.
Ulva lactuca L. var. latissima DC.	f.	o.
Total no. of species: 48	35	37

The *Laminaria Cloustoni* zone could not be properly examined owing to difficulty of access, but ten plants were gathered during both the spring and autumn low tides for examination of the epiphytes on the stipes. A definite zonation of these has already been mentioned by Børgesen (1905), Cotton (1912) and Rees (1935). Table VII shows the zonation of the epiphytes on the Castletown specimens. There was little difference between the epiphytic growth of spring and autumn.

Table VII. *Zonation of epiphytes on stipes of* Laminaria Cloustoni

Species	Abundance	Distance in cm. from base of stipe (70 cm. high)
Acrochaetium virgatulum J. Ag.	f.	0–63
Cladophora rupestris Kütz.	a.	0–63
Delesseria alata Lamour.	a.	0–51
Dermatolithon macrocarpum Fosl. var. Laminariae Fosl.	a.	0–62
Ectocarpus fasciculatus Harv. var. typica J. Ag.	f.	63–70
Phycodrys rubens Batt.	f.	0–16
Polysiphonia urceolata Grev. var. typica J. Ag.	a.	8–65
Ptilota plumosa Ag.	f.	0–41
Ptilothamnion pluma Thur.	o.	10–13
Rhodymenia palmata Grev. var. marginifera Harv.	a.	0–62

A rich undergrowth of Rhodophyceae showing little seasonal change occurs throughout the *L. digitata* and the upper part of the *L. Cloustoni* zones on the ledges. The most abundant of these are the calcareous species *Lithothamnion polymorphum* and *Corallina officinalis*, while many delicate red forms grow as epiphytes on *Corallina*. The following are found as undergrowth species on the ledges:

Abundant

Corallina officinalis
Lithothamnion polymorphum
Nitophyllum ramosum

Frequent

Acrochaetium virgatulum
Ceramium rubrum
Chondrus crispus
Cladophora rupestris
Cruoria pellita
Delesseria alata
Halurus equisetifolius
Melobesia minutula
Phycodrys rubens
Polysiphonia urceolata var. typica
Rhodymenia palmata var. marginifera

Occasional

Callithamnion brachiatum
C. Hookeri
C. tetragonum
Callophyllis laciniata
Chlorochytrium immersum
Delesseria hypoglossum
D. ruscifolia
Dilsea edulis
Euthora cristata
Griffithsia flosculosa
Laurencia pinnatifida
Plocamium coccineum
Ptilota plumosa
Rhodophyllis bifida

L. *Community hanging under ledges*

A characteristic shade vegetation occurs on the underside of projecting ledges in the lower littoral and sublittoral regions. There is little seasonal variation in such vegetation and the following species are usually present:

Cladophora rupestris
Corallina officinalis
Delesseria alata
Laurencia pinnatifida
Lithothamnion polymorphum
Lomentaria articulata
Melobesia minutula
Plumaria elegans
Rhodochorton Rothii
Rhodymenia palmata var. marginifera

M. *Pool vegetation*

Numerous rock pools occur throughout the area. Those on the ledges towards the south are mainly small, usually under 8 in. in depth and of the "coralline" type, i.e. containing a plentiful calcareous growth of *Corallina* and *Lithothamnion*. These shallow pools furnish a rich algal flora, the most

characteristic species being given in Table VIII together with their vertical distribution, abundance and seasonal occurrence.

Table VIII. *Vegetation of shallow "coralline" rock pools*

Species	Season	Level: +8 to +4 ft.	0 ft. +4 to 0 ft.	0 to −4 ft.	−4 to −8 ft.
Callithamnion arbuscula Lyngb.	Sp.	—	—	f.	f.
	S.	—	—	f.	f.
	A.	—	o.	f.	f.
	W.	—	o.	o.	f.
C. brachiatum Bonnem.	Sp.	—	—	—	o.
	S.	—	—	—	—
	A.	—	—	o.	o.
	W.	—	—	o.	o.
C. Hookeri Ag.	Sp.	—	o.	f.	f.
	S.	—	—	f.	f.
	A.	—	f.	f.	f.
	W.	—	f.	f.	f.
Ceramium ciliatum Ducluz.	Sp.	o.	o.	f.	o.
	S.	—	o.	f.	f.
	A.	—	f.	o.	o.
	W.	—	o.	o.	—
C. rubrum Ag.	Whole year	f.	f.	f.	f.
Chaetomorpha tortuosa Kütz.	Sp.	a.	f.	o.	o.
	S.	a.	a.	f.	o.
	A.	o.	o.	o.	o.
	W.	o.	o.	o.	—
Chondrus crispus Stackh.	Whole year	o.	o.	o.	o.
Chylocladia kaliformis Hook.	Sp.	o.	o.	o.	f.
	S.	—	o.	o.	f.
	A.	—	o.	o.	f.
	W.	—	o.	o.	o.
C. ovata Batt.	Sp.	—	f.	f.	f.
	S.	—	o.	f.	f.
	A.	—	o.	o.	o.
	W.	—	f.	f.	f.
Cladophora albida Kütz.	Sp.	—	—	—	—
	S.	o.	f.	f.	f.
	A.	—	—	—	—
	W.	—	—	—	—
C. rupestris Kütz.	Whole year	f.	f.	f.	f.
C. sericea Kütz.	Sp.	a.	a.	—	—
	S.	a.	f.	—	—
	A.	o.	—	—	—
	W.	f.	o.	—	—
Codium tomentosum Stackh.	Sp.	o.	f.	o.	o.
	S.	—	f.	o.	o.
	A.	o.	f.	o.	o.
	W.	o.	f.	o.	o.
Colpomenia sinuosa Derb. et Sol.	Sp.	o.	o.	o.	o.
	S.	—	—	—	o.
	A.	—	o.	o.	o.
	W.	o.	o.	—	—
Corallina officinalis L.	Whole year	a.	a.	a.	a.
Cystoclonium purpureum Batt.	Sp.	—	o.	o.	o.
	S.	—	—	o.	f.
	A.	—	—	o.	f.
	W.	—	o.	o.	o.

Table VIII (*contd.*)

Species	Season	Level: +8 to +4 ft.	+4 to 0 ft.	0 to −4 ft.	−4 to −8 ft.
Dumontia incrassata Lamour.	Sp.	f	f.	f.	f.
	S.	—	—	—	—
	A.	—	—	—	—
	W.	—	—	—	—
Ectocarpus confervoides Le Jol.	Sp.	a.	a.	f.	f.
	S.	f.	f.	f.	—
	A.	f.	o.	—	—
	W.	f.	o.	—	—
Enteromorpha clathrata J. Ag. var. genuina Batt.	Sp.	f.	f.	o.	—
	S.	a.	a.	o.	—
	A.	a.	f.	o.	—
	W.	f.	o.	o.	—
E. compressa Grev.	Sp.	f.	f.	o.	—
	S.	f.	f.	o.	—
	A.	f.	o.	o.	—
	W.	o.	o.	—	—
E. Linza J. Ag. var. lanceolata (Kütz.)	Sp.	o.	f.	f.	—
	S.	—	—	—	—
	A.	—	—	—	—
	W.	—	—	—	—
Fucus serratus L.	Whole year	o.	f.	f.	f.
Gelidium corneum Lamour.	Whole year	o.	o.	f.	f.
Griffithsia flosculosa Batt.	Sp.	—	—	—	f.
	S.	—	—	o.	f.
	A.	—	—	—	f.
	W.	—	o.	o.	f.
Halurus equisetifolius Kütz.	Sp.	—	—	—	o.
	S.	—	—	—	o.
	A.	—	—	—	o.
	W.	—	—	o.	o.
Heterosiphonia plumosa Batt.	Sp.	—	—	o.	f.
	S.	—	—	—	f.
	A.	—	—	o.	f.
	W.	—	—	o.	f.
Laminaria digitata Lamour.	Whole year	—	o.	o.	f.
Laurencia hybrida Lenor.	Sp.	o.	f.	f.	f.
	S.	o.	o.	f.	f.
	A.	o.	o.	o.	f.
	W.	o.	f.	f.	f.
L. pinnatifida Lamour.	Sp.	—	o.	o.	f.
	S.	—	o.	o.	o.
	A.	—	o.	o.	f.
	W.	—	o.	o.	f.
Leathesia difformis Aresch.	Sp.	—	—	—	—
	S.	f.	f.	f.	f.
	A.	—	o.	o.	o.
	W.	—	—	—	—
Lithophyllum incrustans Fosl.	Whole year	—	f.	o.	o.
Lithothamnion Lenormandi Fosl.	Whole year	f.	f.	—	—
L. lichenoides Fosl.	Whole year	—	o.	f.	f.
L. polymorphum Aresch.	Whole year	—	—	o.	a.
Monostroma Grevillei Wittr.	Sp.	a.	f.	f.	f.
	S.	—	—	—	—
	A.	—	—	—	—
	W.	—	—	—	—

Table VIII (*contd.*)

Species	Season	Level: +8 to +4 ft.	+4 to 0 ft.	0 to −4 ft.	−4 to −8 ft.
Nitophyllum ramosum Batt.	Sp.	—	—	o.	f.
	S.	—	—	—	f.
	A.	—	—	—	f.
	W.	—	o.	—	f.
Phycodrys rubens Batt.	Sp.	—	—	o.	o.
	S.	—	—	—	o.
	A.	—	—	—	—
	W.	—	—	—	o.
Phyllitis fascia Kütz. var. genuina Batt.	Sp.	f.	f.	o.	o.
	S.	—	—	—	—
	A.	—	—	—	—
	W.	o.	o.	—	—
Polysiphonia nigrescens Grev.	Sp.	f.	f.	f.	—
	S.	o.	f.	f.	—
	A.	o.	f.	a.	—
	W.	o.	f.	f.	—
P. urceolata Grev. var. typica J. Ag.	Sp.	o.	o.	o.	o.
	S.	—	—	o.	—
	A.	—	o.	—	—
	W.	o.	o.	—	o.
Pterosiphonia parasitica Schm.	Whole year	—	—	—	o.
P. thuyoides Schm.	Sp.	—	—	f.	f.
	S.	—	—	f.	f.
	A.	—	f.	f.	o.
	W.	—	f.	f.	o.
Pylaiella littoralis Kjellm.	Sp.	f.	f.	f.	f.
	S.	f.	o.	f.	—
	A.	f.	f.	f.	f.
	W.	f.	f.	—	—
Rhodomela subfusca Ag.	Sp.	o.	f.	f.	o.
	S.	o.	f.	o.	o.
	A.	o.	f.	o.	f.
	W.	o.	f.	o.	f.
Scytosiphon lomentarius J. Ag.	Sp.	a.	a.	f.	o.
	S.	f.	f.	o.	o.
	A.	f.	a.	o.	o.
	W.	a.	f.	—	o.
Sphacelaria cirrhosa Ag. var. fusca Holm. et Batt.	Whole year	a.	f.	o.	o.
Ulva lactuca L. var. latissima DC.	Sp.	o.	f.	f.	f.
	S.	o.	o.	f.	f.
	A.	o.	o.	o.	f.
	W.	o.	o.	o.	f.

Several large and deeper pools (up to 1·5 ft. in depth) occur from 0 to +5 ft. in the central part of the area where the slope is gentler. They contain deposits of pebbles and a little sandy mud and have a characteristic flora differing considerably from that of the "coralline" pools. The species present are given in Table IX (p. 114).

II. Communities of sand and pebbles

N. *Enteromorpha* community

In the extreme northern part of the area a large part of the gently sloping shore between +5 and +9 ft. is strewn with stones and pebbles mixed with some sandy mud. On this substratum a rich and almost pure growth of

Table IX. *Vegetation of large, moderately deep pools above mean sea-level*

Species	Sp.	S.	A.	W.
Acrochaetium virgatulum J. Ag.	o.	f.	f.	f.
Asperococcus fistulosus Hook.	f.	a.	f.	o.
Calothrix confervicola Ag.	f.	f.	a.	f.
Ceramium rubrum Ag.	a.	a.	f.	f.
C. strictum Harv.	—	a.	—	—
Chaetomorpha aerea Kütz.	f.	o.	a.	f.
Chorda filum Stackh.	—	a.	a.	o.
Chordaria flagelliformis Ag.	—	f.	f.	o.
Cystoclonium purpureum Batt.	f.	f.	—	o.
Dictyosiphon foeniculaceus Grev.	—	f.	f.	—
Dumontia incrassata Lamour.	f.	—	—	o.
Ectocarpus confervoides Le Jol.	a.	f.	f.	—
E. siliculosus Kütz.	—	f.	f.	o.
Enteromorpha compressa Grev.	f.	f.	f.	f.
Eudesme virescens (Carm.) J. Ag.	—	f.	—	—
Fucus serratus L.	f.	f.	f.	f.
Halidrys siliquosa Lyngb.	o.	o.	o.	o.
Laminaria digitata Lamour. var. typica Fosl.	o.	o.	o.	o.
L. saccharina Lamour.	o.	o.	o.	o.
Leathesia difformis Aresch.	—	f.	—	—
Litosiphon filiformis Batt.	o.	—	—	—
L. pusillus Harv.	—	f.	f.	—
Monostroma Grevillei Wittr.	f.	—	—	—
Myrionema strangulans Grev. var. typica Batt.	—	a.	f.	o.
Myriotrichia clavaeformis Harv.	—	f.	o.	—
M. filiformis Harv.	—	f.	o.	—
Phyllitis fascia Kütz. var. genuina Batt.	f.	—	—	o.
Polysiphonia nigrescens Grev.	f.	—	f.	f.
Pylaiella littoralis Kjellm.	f.	f.	f.	f.
Rhodomela subfusca Ag.	f.	f.	f.	a.
Scytosiphon lomentarius J. Ag.	a.	o.	a.	a.
Sphacelaria cirrhosa Ag. var. pennata Hauck	f.	o.	f.	f.
Ulva lactuca L. var. latissima DC.	a.	f.	f.	f.

Enteromorpha intestinalis grows. Young plants of *E. intestinalis* occur in winter, attain their maximum growth in spring and early summer and have decreased considerably by autumn. Occasional plants of *Monostroma Grevillei* and a little *Ulothrix implexa* occur along with *Enteromorpha intestinalis* in spring. The existence of the community is to a large extent due to the brackish conditions in this part of the area caused by the entrance of a stream.

This characteristic community is common on British coasts, where its occurrence is invariably associated with low salinity. Cotton (1912) has described a similar *E. intestinalis* community on a rocky substratum. Børgesen (1905) found the community in the Faeröes both on rock and, at the inner end of bays and inlets, on gravel and stones.

O. *Sand-pool vegetation*

Most of the pools close to the sandy bay at the north of the area contain a considerable quantity of sand. A very rich growth of typically psammophilous species inhabits these pools. Most of the algae are partly buried in the sand and are attached either to rock beneath or to pebbles; heavy epiphytic growths are borne by several of the species such as *Halidrys*, *Ahnfeldtia*,

Polyides and *Chondrus*. The characteristic species of sand-pools lying between mean low water of neap and spring tides (−5 to −9 ft.) are given in Table X.

Table X. *Vegetation of sublittoral sand-pools*

Species	Sp.	S.	A.	W.
Ahnfeldtia plicata Fries	f.	f.	f.	f.
Asperococcus fistulosus Hook.	o.	a.	—	—
Callithamnion corymbosum Lyngb.	—	—	f.	—
Ceramium ciliatum Ducluz.	o.	o.	f.	—
C. rubrum Ag.	f.	f.	a.	f.
C. strictum Harv.	—	a.	—	—
Chondrus crispus Stackh.	f.	f.	f.	f.
Chorda filum Stackh.	—	a.	f.	—
Chordaria flagelliformis Ag.	o.	f.	f.	—
Chylocladia kaliformis Hook.	o.	f.	f.	f.
C. ovata Batt.	o.	o.	o.	o.
Cladophora albida Kütz.	—	f.	—	—
C. Hutchinsiae Harv.	f.	a.	f.	f.
C. lanosa Kütz.	o.	f.	—	—
C. rupestris Kütz.	f.	f.	f.	f.
Cladostephus spongiosus Ag.	o.	o.	o.	o.
Colpomenia sinuosa Derb. et Sol.	o.	—	o.	—
Cystoclonium purpureum Batt.	o.	f.	f.	o.
Delesseria alata Lamour.	f.	o.	—	—
D. hypoglossum Lamour.	f.	—	f.	f.
Dictyota dichotoma Lamour.	a.	a.	a.	f.
Dumontia incrassata Lamour.	o.	—	—	—
Ectocarpus siliculosus Kütz.	f.	—	f.	—
Enteromorpha compressa Grev.	o.	f.	f.	f.
Fucus serratus L.	f.	f.	f.	f.
Furcellaria fastigiata Lamour.	a.	a.	a.	a.
Gelidium latifolium Born.	o.	o.	o.	o.
Griffithsia corallinoides Batt.	—	—	f.	f.
G. flosculosa Batt.	f.	—	f.	f.
Halidrys siliquosa Lyngb.	f.	f.	f.	f.
Halurus equisetifolius Kütz.	f.	o.	f.	f.
Heterosiphonia plumosa Batt.	f.	o.	f.	f.
Laminaria digitata Lamour. var. typica Fosl.	f.	f.	f.	f.
L. saccharina Lamour.	f.	f.	f.	f.
Laurencia pinnatifida Lamour.	o.	—	—	o.
Leathesia difformis Aresch.	—	a.	f.	—
Litosiphon Laminariae Harv.	f.	—	—	—
L. pusillus Harv.	—	f.	f.	—
Mesogloia vermiculata Le Jol.	—	f.	o.	—
Monostroma Grevillei Wittr.	f.	—	—	—
Myrionema strangulans Grev. var. typica Batt.	o.	f.	f.	—
Nitophyllum ramosum Batt.	f.	f.	f.	f.
Phyllitis fascia Kütz. var. genuina Batt.	f.	—	—	—
Plocamium coccineum Lyngb.	o.	—	o.	f.
Polyides rotundus Grev.	a.	a.	a.	a.
Polysiphonia elongata Grev.	f.	f.	o.	f.
P. fruticulosa Spreng.	f.	—	o.	f.
P. nigrescens Grev.	f.	f.	f.	f.
Punctaria plantaginea Grev.	o.	—	—	—
Pylaiella littoralis Kjellm.	f.	f.	f.	—
Rhodomela subfusca Ag.	f.	f.	a.	a.
Scytosiphon lomentarius J. Ag.	a.	o.	o.	o.
Spermothamnion Turneri Aresch.	f.	—	—	a.
Sphacelaria bipinnata Sauv.	o.	a.	a.	o.
S. cirrhosa Ag. var. pennata Hauck	a.	a.	a.	a.
Ulva lactuca L. var. latissima DC.	a.	f.	a.	f.

A different type of sand-pool vegetation occurs in certain pools at higher levels where the salinity is kept low by the entrance of fresh water. This vegetation shows marked seasonal changes and the predominating species

belong to the Chlorophyceae and Phaeophyceae. The most typical and abundant species are

Monostroma Grevillei	Pylaiella littoralis
Enteromorpha intestinalis	Leathesia difformis
Ulva lactuca var. latissima	Chorda filum
Chaetomorpha aerea	Ceramium strictum
Cladophora rupestris	Dumontia incrassata
C. sericea	Polyides rotundus
Dictyosiphon foeniculaceus	

P. *Sublittoral community on pebbles*

This community occurs in the sublittoral part of the sandy bay at the north of the area. The species are all attached to stones and pebbles scattered on the sand throughout this part of the bay. The majority of species occurring here are the same as those given in Table X for the sublittoral sand-pools adjoining the bay but their distribution in this community is more scattered.

Cotton (1912) and Rees (1935) have described communities in Ireland similar in character though differing somewhat in floristic composition.

Conclusion

The study of the vegetation in the survey area in Castletown Bay has resulted in the recognition of fifteen communities distinctive of the different types of habitat, e.g. rock, sandy mud-covered rock, pebbles, sand and pools. Of these communities the *Porphyra-Urospora-Ulothrix* community, the *Laurencia-Lomentaria* community, the *Laurencia-Cladophora-Rhodochorton* community and *Enteromorpha-Cladophora-Chordaria* community have not been previously recognized.

The communities described are all perennial except two, namely, the *Porphyra-Urospora-Ulothrix* community and the *Enteromorpha-Cladophora-Chordaria* community, the former occurring only in winter and spring and the latter in spring and summer. Many of the perennial communities, however, include such a large number of annual and short-lived species that the composition of any community is usually undergoing changes. This is best illustrated in the case of the *Laurencia-Lomentaria* community (p. 103). The communities which exhibit least seasonal change are (1) the *Laminaria* community, and (2) the community hanging under ledges, the floristic composition of which remained remarkably constant throughout the year.

The horizontal distribution of the vegetation in the area is chiefly influenced by the degree of exposure to wave action. The vegetation in the southern more exposed part of the area differs noticeably from the northern more sheltered part. Several communities are restricted to the southern part, e.g. the *Himanthalia* community, the *Laurencia-Lomentaria* community and the *Porphyra-Urospora-Ulothrix* community, while those occurring on movable substrata such as sand or pebbles are confined to the most sheltered northern part. The effect of exposure is also very marked in the size and development

of species of Fucaceae, such as *Ascophyllum* and *Fucus vesiculosus* which occur throughout the whole area.

Owing to the large tidal range and gentle slope many of the communities cover large areas of shore. This is carried to an extreme in the north of the area where the slope is gentlest and such communities as the *Enteromorpha* community, the sublittoral community on pebbles and the *Laminaria* community occupy very large intertidal areas strewn with sand, pebbles and boulders. In these gently sloping places the boundaries of the communities are not nearly so clearly defined as on the steeper ground towards the south.

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THE EFFECT OF TEMPERATURE AND LIGHT INTENSITY ON THE RATE OF APPARENT ASSIMILATION OF *FUCUS SERRATUS* L.[1]

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(*With seven Figures in the Text*)

CONTENTS

Introduction

It is well known that the conditions of light and temperature under which a plant has been growing have a considerable effect on the subsequent assimilation rate under any given conditions.

In general, typical sun plants show an increasing assimilation rate with rising light intensity, including full summer sunlight (as in *Nasturtium palustre* or *Atriplex latifolium*; Lundegårdh, 1921): while typical shade plants (like *Stellaria nemorum*, Lundegårdh, 1921) do not increase their assimilation rate when exposed to natural illumination brighter than 1/28th to 1/5th total summer daylight, and some deep shade plants (such as *Trichomanes*, Montfort & Neydel, 1928; *Rhodymenia palmata*, Montfort, 1929*a*) may even show a slower rate at high light intensities than at lower ones. Lundegårdh also found that the "light minimum" (defined as the lowest value of illumination at which assimilation can just out-balance respiration at ordinary temperatures) was 1/60th total summer daylight for sun plants, while in shade plants it was about 1/120th of the same light. In other words, the range of utilization of daylight varies considerably with the previous "light climate".

[1] An abbreviation of a thesis accepted for M.Sc. (Lond.) July 1936.

This question of sun and shade plants is of much interest when considering algae of the littoral zone, because they are subject to great variations of light during their submerged and exposed periods. Montfort (1929 *a*) considered that in its reaction to light, *Fucus vesiculosus* behaved as a sun plant: Ehrke (1931) regarded the algae which grow fairly high up on the shore—such as *F. serratus* and *Cladophora* spp.—as sun plants, while those red algae which grow at or near low tide level and which are submerged for the greater part of the day behaved as shade plants in their relation of assimilation to light. In their experiments, however, no consideration is paid to temperature when discussing the "light place" of the plants. In the experiments of Lampe with *Fucus serratus* (1935), the so-called "light place" was correlated with seasonal variations of temperature.

OBJECT OF THE PRESENT SERIES OF EXPERIMENTS

In the following experiments an attempt has been made to explore further the effect of light and temperature on the rate of apparent assimilation of *F. serratus*, using only material which has been kept under standardized conditions during the pre-experimental period. Each frond of *F. serratus* was selected on the shore from the same zone, kept for 5 days in diffuse daylight, darkened for 12 hours on the night previous to experimentation, and subjected to the same degree of illumination prior to the experimental period. Also, as each of my experiments extended for a period of 9 hours, they give a truer picture of what occurred than could be obtained by taking a single and variable short period in material not previously standardized (as in Ehrke's experiments).

The importance of this may be seen from the work of Harder (1925, 1930, 1933) who has shown that the previous history of the plant is of great importance in determining its subsequent reaction to light and temperature. For instance, in *Cladophora* and *Fontinalis* a certain time must elapse on exposure to light after darkness before the maximum assimilation rate is reached, the rate rising gradually from an initial low value during the first 1–4 hours, according to the experimental conditions. With *Elodea*, which generally reacts as a sun plant, Harder (1933) obtained shade-adapted forms by keeping sun plants in dim light in the laboratory for about 4 weeks.

MATERIAL AND METHODS

Young non-fertile plants of *Fucus serratus* about 1 ft. in length were gathered on the shore at Bexhill from the middle of the *F. serratus* zone and brought to London in a damp condition. Small tips, generally with two dichotomies, were taken, and the surface area of each such frond found by tracing the outline on paper, cutting out, weighing and comparing the weight with that of a known area of similar paper. The rate of apparent assimilation was always calculated per 100 sq. cm. of frond.

The area was adopted as a basis because it was realized that the dry weight (or even fresh weight) of a frond varies according to the amount of assimilation that has taken place. The dry weight also can only be determined at the end of a series of experiments, as it involves killing the frond. After a series of experiments on a frond in bright light the dry weight would be appreciably greater than after a series on the same frond in dim light.[1]

The method adopted was the determination of the amount of dissolved oxygen given out by the plant in a known time, using Winkler's method. This consists in absorbing the dissolved oxygen, which is contained in a measured volume of the water, by adding to the water a little manganous chloride solution and then a mixture of solutions of alkaline hydroxide and potassium iodide in a vessel which is completely filled with the liquids and is closed from the air. The oxygen dissolved in the water will then convert a part of the precipitated manganous hydroxide into the higher hydroxide. Hydrochloric acid is now added in excess, and the acid mixture is allowed to stand. After a time the iodine liberated by the higher manganese hydroxide is titrated with standard thiosulphate solution. From the amount of iodine thus found the percentage of dissolved oxygen can be calculated.[2] In the following experiments, the thiosulphate used was $N/100$ and the accuracy tested from time to time was usually within 2%, the margin of error increasing to 6% on the smallest values obtained.

This method was chosen in preference to the measurement of the rate of carbon dioxide intake, partly because by this means small changes of oxygen concentration can be measured accurately, partly because it requires no stream of gas to pass over the plant, which can remain submerged in its natural medium, i.e. sea water.[3] By this method, it is also possible to work within a narrow range of pH which is within that tolerated by *Fucus* (p. 121).

The apparatus as finally used consisted of an assimilatory chamber enclosed in a rectangular glass water-bath, illuminated from two opposite sides

[1] Moreover, the dry weight was found to be unevenly distributed over apparently similar pieces of frond.

[2] For details of the method see Clowes & Coleman, *Quantitative Chemical Analysis*, 1931, p. 386.

[3] Preliminary experiments have been carried out using the rate of change of pH of a solution, due to absorption of CO_2 (determined by change of colour of an indicator), as a measure of the assimilation rate of *F. serratus*, a stream of CO_2-enriched air being circulated in an enclosed system by means of a mercury circulating pump. Even with air saturated with water vapour the *Fucus* frond gradually became drier as water was withdrawn from it by the stream of gas, until eventually it died. Bubbling the air through the assimilatory chamber when the latter was three-quarters full of sea water (so that the plant was completely submerged) was more satisfactory, but the pH of the sea water then varied between somewhat wide limits. Although the pH of water in rock pools can vary to a considerable extent (from excess CO_2 where animal life predominates to its absence in pools crowded with plant life and exposed to bright light), the pH of the moving water with which the *Fucus* is covered at high tide varies only slightly daily and at different seasons.

by two Osram gas-filled pearl electric lamps, of similar wattage and age. Different light intensities were obtained by using lamps of different strengths (namely 40, 100, 200, 500 and 1000 W.). The main illumination was normal to the plant, so that the middle of the beam of light corresponded to the middle of the plant. As the beam covered a very much larger area than that of the assimilatory chamber, it could be assumed that all the surface of the frond received light of the same intensity. The water-bath and lamps were darkened to prevent any external light from entering. The assimilation chamber took the form of a flat-sided glass bottle, holding about 150 c.c., and with a closely fitting stopper. Before use, the capacity of the bottle was accurately determined.

A piece of non-fertile *Fucus*, occupying about 2–3 c.c., and of known surface area, was put into the experimental bottle, *B*, which was then filled with sea water from a large bottle, *R*, in which some other *Fucus* had been allowed to respire overnight (in the dark), thus removing oxygen, so that, on assimilation, the water did not become supersaturated with oxygen and cause bubbles to be formed. (This method of removing oxygen had previously been found to be satisfactory by blank experiments.) The water in bottle *R* was used to fill the experimental bottle *B*, and at the same time a similar bottle, *A*, of known capacity, was also filled from it, the "respiring" bottle *R* being stoppered and gently shaken before its contents were added to the two experimental bottles, so that both received water of the same composition.

The experimental bottle *B* containing the *Fucus* was then put in the illuminated water-bath, so that the flat surfaces of the frond were exposed to the lights, and the plant allowed to assimilate, the temperature being kept constant to within 0·5° C. by running water, or by the addition of ice or of cold water. After a period of exposure to light (generally 2 hours), at a fixed temperature, the frond was removed from bottle *B*, and the oxygen content of the water in the two bottles *A* and *B* determined, the difference between them giving the amount of apparent assimilation that had taken place. Two more bottles, *C* and *D*, the latter containing the same piece of *Fucus* as was used before, were filled meanwhile from a second "respiratory" bottle, R_2, and *D* was then illuminated as before, and at the same temperature, for a further experimental period.[1]

Consequently the *Fucus* had a new supply of deoxygenated, CO_2-enriched sea water every 2 hours. It is believed that the free CO_2 thus provided was more than sufficient for the 2 hours that each experiment lasted. This is supported by the fact that the *p*H of the sea water after the assimilatory period was 8·0–8·1, rather less than that of ordinary sea water (8·1–8·2). The *p*H of

[1] The time taken for the transference of the *Fucus* frond from bottle *B* to bottle *D* was 2–3 min. only, bottles *C* and *D* being filled with sea water as soon as the $MnCl_2$ and KOH and KI (p. 120) had been added to *A* and *B*. Consequently the frond was in ordinary daylight for 2 min. between each experimental period.

the sea water was found to be 8·45 after all the free CO_2 had been removed by prolonged boiling;[1] thus it appears that some free CO_2 was still present after each experiment. It is well known that sea water contains bicarbonates in solution and it is believed that these form a reserve of CO_2 upon which the plant can draw if necessary during active assimilation (cf. James, 1928). For these reasons, it is assumed that CO_2 was always in excess under the conditions of these experiments.

At first 1 hour's exposure to light at the experimental temperature was given (Fig. 1, Series 1), during which time the rate of assimilation was not measured, allowing the plant to become accustomed to the conditions. After the first series of experiments, however, the rate of apparent assimilation during this initial hour was measured, and subsequently over 2-hourly periods for a further period of 8 hours, the plant being kept throughout at constant temperature.

On the next day the experiment was repeated at a different temperature but at the same light intensity, and so on, until a number of different temperatures had been employed (usually 5, 15 and 25° C., and sometimes also 10, 20 and 30° C.).

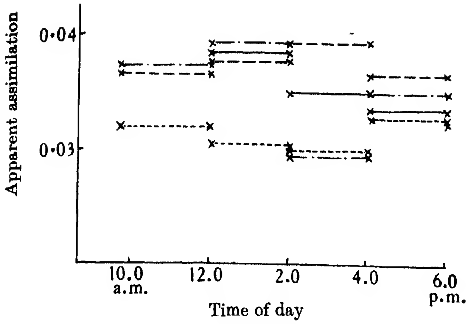
Plants were sent by post from Bexhill immediately after gathering. On their arrival, selected pieces in good condition were placed in a large bowl of clean sea water standing in a cool room in front of a north window. The temperature of this room was 10–12° C. and the illumination at midday varied from 10% (on dull days) to 20% (in sunny weather) of external bright daylight.

On the fifth day, the plant was given artificial illumination from dusk until 9 p.m. and was darkened for 12 hours. Experiments started at 9.30 a.m. and the experimental pieces had continuous illumination from 9.30 a.m. until 6.40 p.m. at the temperature of the experiment. The pieces were then removed, placed in sea water at 10–12° C., illuminated with electric light (60 W.) until 9.30 p.m. and darkened again for 12 hours as before. The next day, the observations were repeated at another temperature and so on throughout the whole experimental series. These precautions were taken in order to keep the "light history" of each individual similar and to avoid the possible complication of unequal "light adaptation" in the sense of Harder (cf. p. 119).

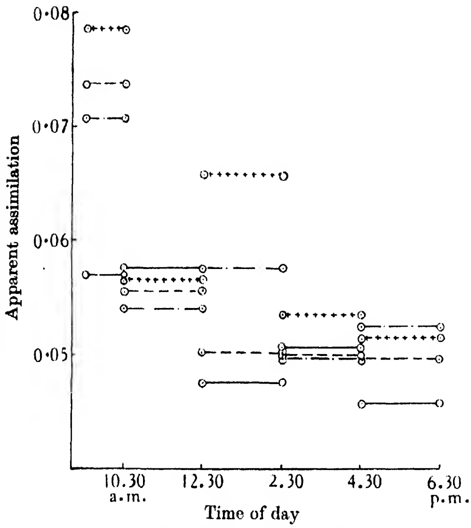
After a temperature series at one light intensity had been carried out (using the same shoot of *Fucus* throughout), the series was repeated at another light intensity, using a new shoot of *Fucus* obtained from Bexhill later than the first and having been kept in the laboratory for a comparable length of time (generally 5 days) at the beginning of the series.

Each series was carried through on successive days as far as possible, using material previously kept for 5 days in an unheated room (temperature 9–10° C.),

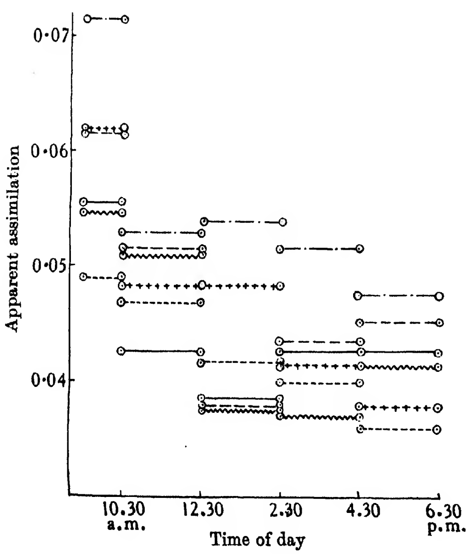
[1] After boiling, the sea water was cooled, made up to the original volume with boiled distilled water and tested with the indicator (cresol red).

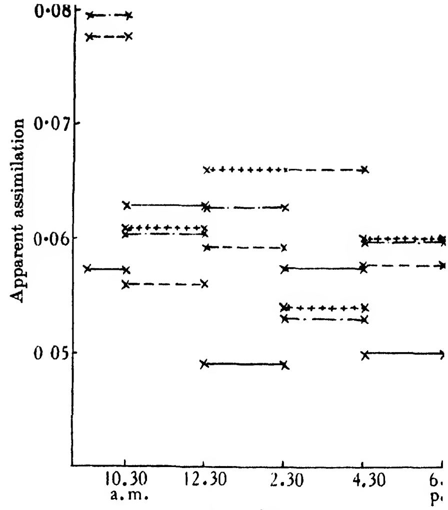


Series I. 2 × 40 W. lamps.

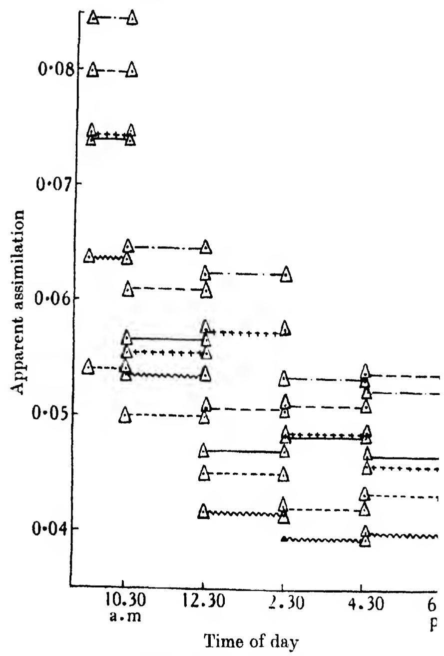


Series II A. 2 × 40 W. lamps.





Series II B. 2 × 40 W. lamps.



Series III B. 2 × 200 W. lamps.

Key

C		C	
5°	- - - - - - -	20°	— — — —
10°	~~~~~~~~	25°	—·—·—
15°	————	30°	++++++++

Note. The rate of apparent assimilation is expresse grams of oxygen per litre liberated per 100 sq. cm. of f

near a north window. Observations on *one* piece of *F. serratus* kept from July 1935 to June 1936 indicate that the level of carbon assimilation is remarkably little influenced by the prolonged artificial conditions. A new piece was used for each light series, however, to avoid any possible harmful after-effect from the exposure to the higher temperatures (25 and 30° C.) of each series. The amount of oxygen evolved is only an indication of apparent assimilation, i.e. the balance between the real assimilation and the respiration under any conditions. There is no satisfactory way at present known of measuring respiration during photosynthesis. When, therefore, the rate of respiration is measured in darkness before and after a period of illumination it is impossible to know how accurately the mean of these figures represents a true value for the rate of respiration during the experimental period of assimilation.[1] Ehrke sometimes divided his material into two halves, and used one for the measurement of assimilation in the light and the other for the simultaneous determination of respiration in darkness, but he does not appear to have investigated the possible variability between the two halves. Experiments with my material suggest that there may be considerable variability (up to 10%) between two apparently identical pieces of *F. serratus* taken from comparable positions on the same plant.

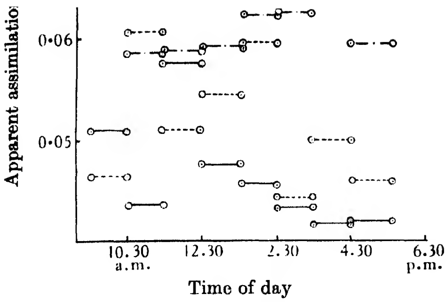
In marine plants (Kniep, 1915, *F. serratus*; Ehrke, 1931, *F. serratus*, *Cladophora*, *Plocamium*), as in land plants, when assimilation and respiration have both been measured, it has been found that temperatures affect the two processes in different degrees. For instance, the respiration rate rises rapidly at higher temperatures (30–40° C.), while the *real* assimilation rate falls at these temperatures, and therefore the *apparent* assimilation rate falls even more quickly.

Estimation of the real assimilation rate therefore does not necessarily show what actually happens inside the plant, while the apparent assimilation rate, which I measured, shows what actual balance of materials there is at each temperature, and it is this *balance* which is of primary importance to the plant.

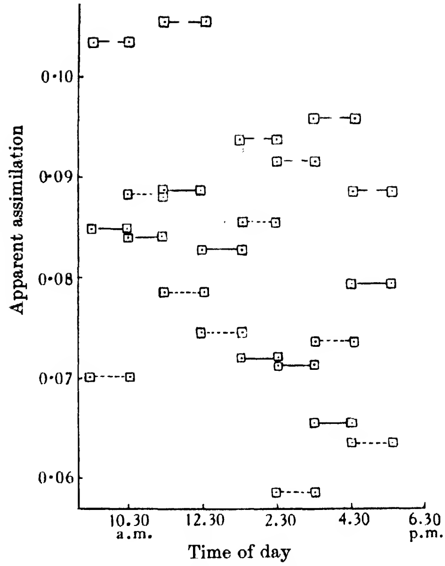
Results

Effect of temperature. It is seen from the graphs in Figs. 1 and 2 that increase in temperature at first causes an increase in the apparent assimilation rate of *Fucus serratus*, the maximum rate generally being at 25° C. if the light is sufficiently bright (i.e. with more than 2×40 W. lamps), there being a fall at 30° C. With low lights (2×40 and 2×100 W. lamps), although rise in temperature from 15 to 25° C. results in an increase in the assimilation rate, there is more apparent assimilation at 5 than at 15° C., both during the first hour of illumination and over the subsequent 8 hours, possibly owing to the lower

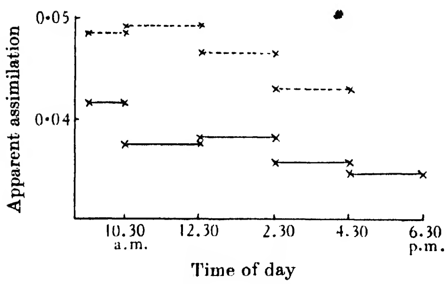
[1] Especially when bright light is used (cf. Briggs, 1933).



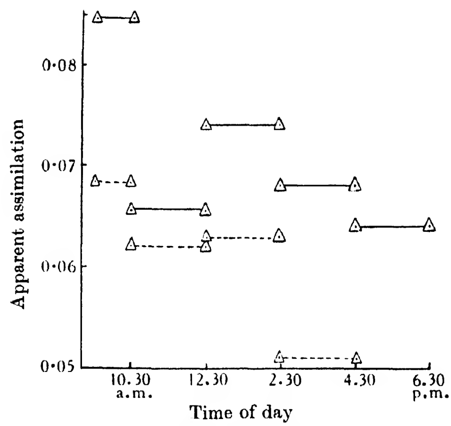
Series IV A. 2 × 100 W. lamps.



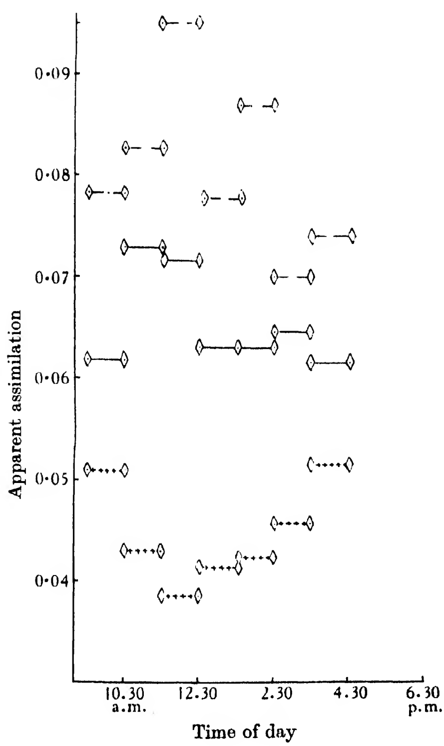
Series IV B. 2 × 500 W. lamps.

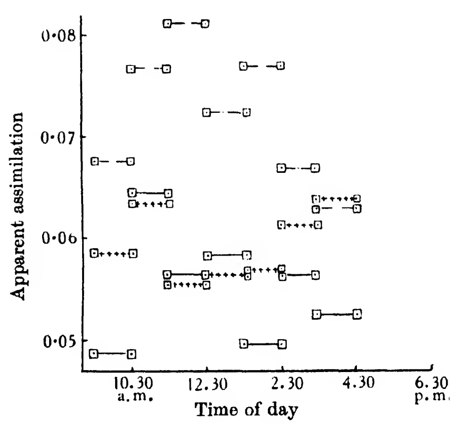


Series V A. 2 × 40 W. lamps.



Series V B. 2 × 200 W. lamps.





temperature retarding the respiration rate to a greater extent than the rate of assimilation, which, although low, continues at the maximum for that light.

With prolonged series of experiments (i.e. 9 hours' illumination), the rate of apparent assimilation (measured at 2-hourly or at hourly intervals) tends, at low light intensities, to fall throughout the day from its initial rate to a value which is independent of the temperature and which is more or less constant for any one light intensity (Figs. 1, 2 and 3). Owing to the larger initial rate at these higher temperatures, with the brighter lights used the drop during the first few hours is more sudden at higher temperatures. If the light is very bright (2×500 W.) the effect of high temperatures can be maintained for a longer period.[1]

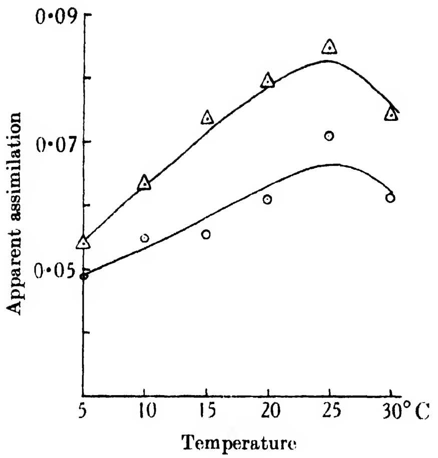
Another suggested explanation of the gradual fall in the rate of apparent assimilation during the day is as follows. Assuming that the *real* assimilating rate is substantially constant under the uniform conditions of the experiment, an increased experimental temperature might cause *progressive* increase in the respiration rate during the first 3 hours. If so, the *apparent* assimilation rate would fall. This is in harmony with the fact that if the experimental temperature is the same as that of the previous existence, there is much less fall in the apparent assimilation rate. The suggestion of increased utilization of internal carbon dioxide with rise in temperature seems equally possible.

In connexion with the optimum temperature for assimilation being 25° C., not higher, it should be noted that the adverse effect of 30° C. is visible *from the first hour* and does not gradually set in during the day.

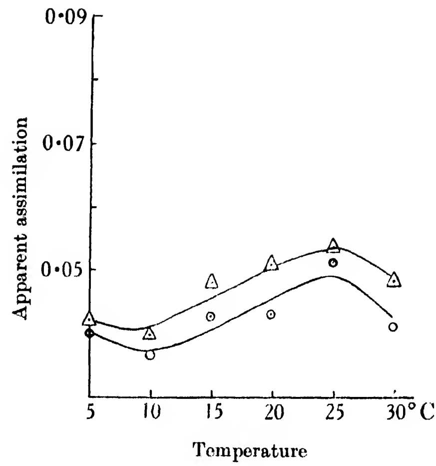
Effect of light. At all temperatures a progressive increase in illumination from 2×40 to 2×500 W. (i.e. 1/14 to 2/3 total daylight[2]) consistently brings about an increase in the apparent assimilation rate—the rate naturally being greater at higher temperatures than at lower ones, except with a very low light intensity (e.g. 2×40 W. lamps), when the low temperature, possibly by checking the respiration rate more than that of assimilation (which is less directly a thermal process), causes the apparent assimilation rate to be greater at 5 than at 15° C. (see also Fig. 4). A light intensity brighter than that of 2×500 W. lamps, e.g. that of 2×1000 W. lamps (equivalent photometrically to full sunlight), causes a decrease in the apparent assimilation rate over the 2×500 W. value, especially at 30° C., where the rate is much below the 15° C. value for this bright light (see Figs. 4 and 5).

[1] The gradual fall during the day might be attributed to an accumulation of the assimilatory products slowing up the assimilation rate. As, however, there is no such fall with 2×500 W. lamps, where the assimilation rate is greatest and where therefore most assimilates are being formed, the gradual fall that occurred at lower light intensities cannot be due to this cause and must be regarded as resulting from the limiting action of the lower light intensities, manifested when a steady state has been attained.

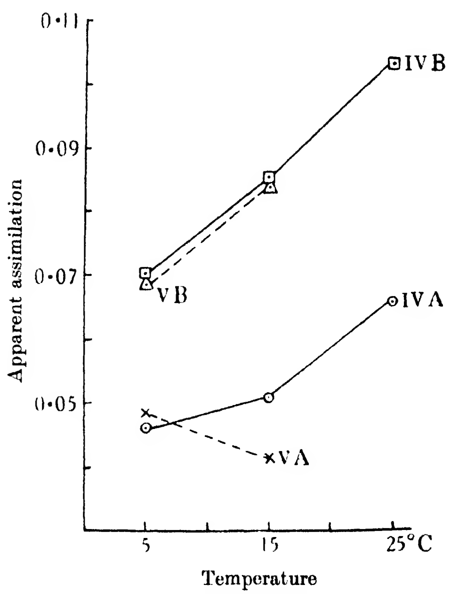
[2] Cf. p. 131.



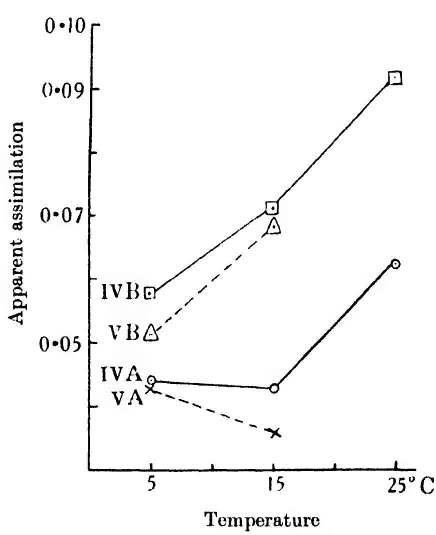
Series III A. 9.30–10.30 a.m. (initial effect).



Series III B. 2.30–4.30 p.m. (after 4–6 hours of illumination).



Series IV C. 9.30–10.30 a.m. (initial effect).



Series V D. 3–4 p.m. (after 5½ hours of illumination).

FIG. 3. Comparison of effect of temperature taken at corresponding times of day. Assimilation values as in Fig. 1.

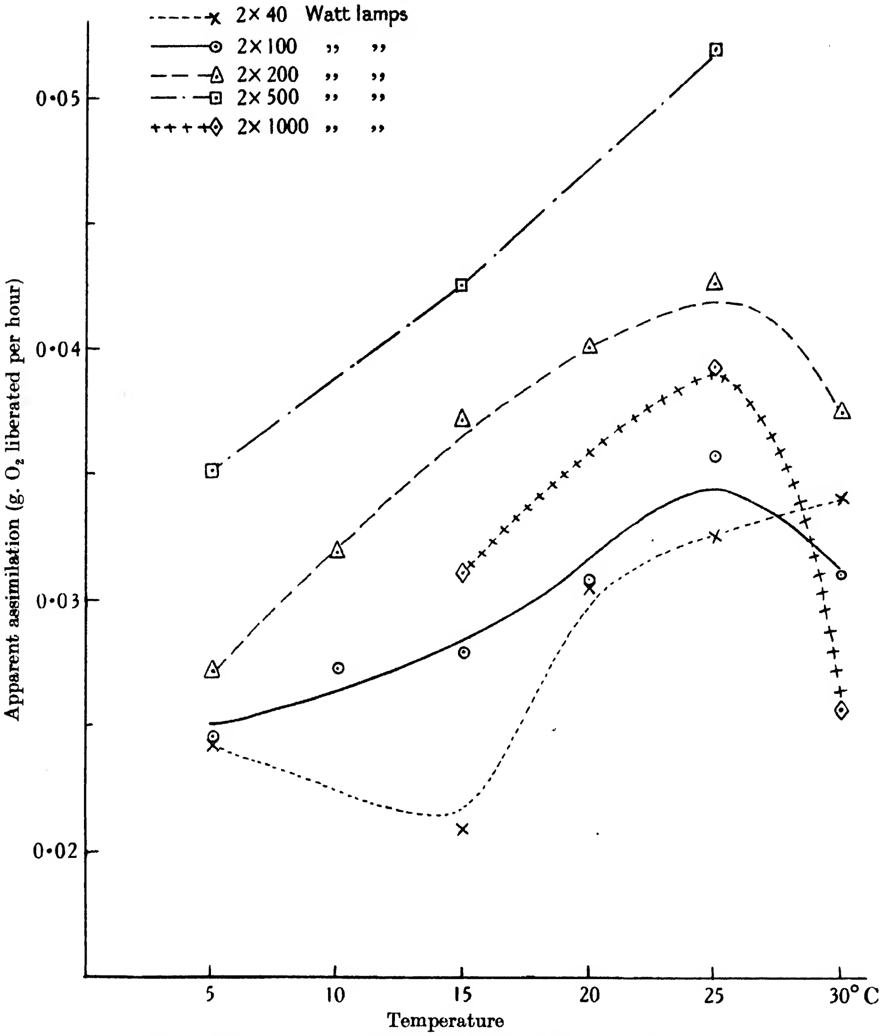


Fig. 4. Effect of temperature during the first hour of illumination.

Table I is constructed from the curves in Fig. 6, for lights up to 2 × 500 W., and shows the tangents of the 5 and 15° C. temperature curves (i.e. the slopes of the — — — — and — · — lines) during the first 3 hours of illumination (from Fig. 6*a*), and after 7 hours' pre-illumination (from Fig. 6*b*).

Table I. *Effects of varying periods of illumination on tangents of assimilation—light intensity curves*

	First 3 hours	After 7 hours' pre-illumination	Ratio first 3 to last 2 hours
5° C.	*ca.* 1/2	*ca.* 1/4	2 : 1
15° C.	*ca.* 1/1	*ca.* 1/2	2 : 1

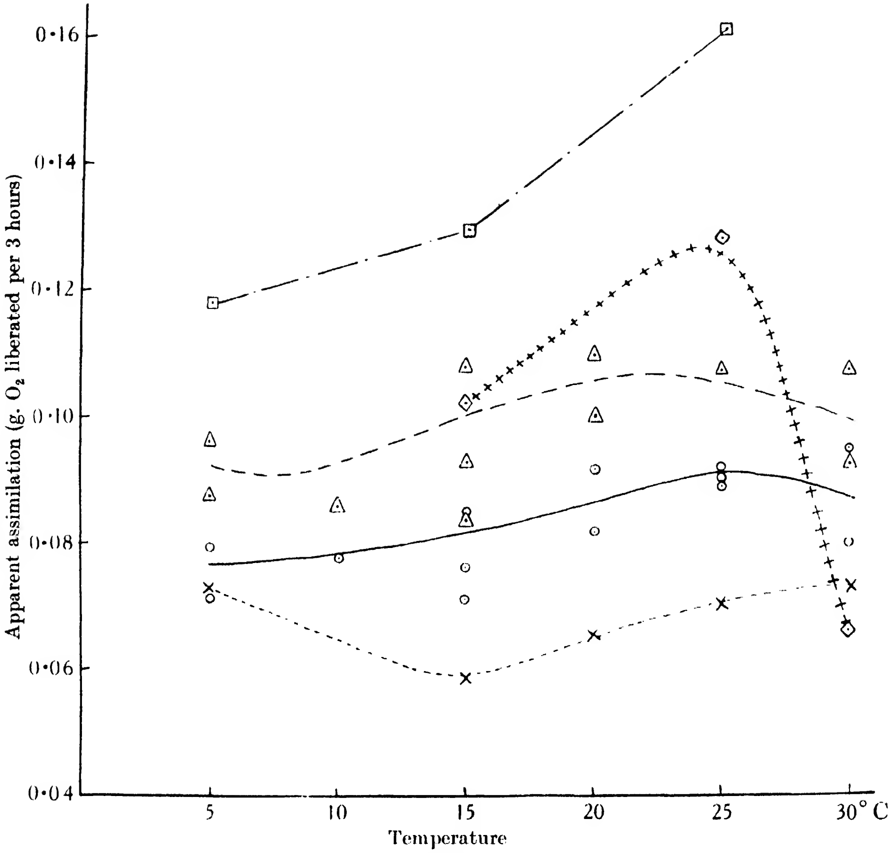


FIG. 5. Effect of temperature during the first 3 hours' illumination at different light intensities. (Symbols as in Fig. 4.)

It is evident from this table that the progressive increase in assimilation rate due to light is greatest in the first 3 hours of illumination, being then about double the increase after 7 hours' pre-illumination, probably because the plants become accustomed to the light in the day as the effect of the change from darkness to the experimental light intensity passes off. The influence of 12 hours' darkness as a pre-illumination period would probably repay further study (cf. Briggs, 1933).

In these experiments there is a simple almost linear relation between light intensity and illumination at any one temperature, until the very bright light of 2 × 1000 W. lamps lowers the rate of assimilation.

The combined effects of temperature and illumination have been expressed in the form of a model. Unfortunately the series of observations with 1000 W. lamp at 5° C. remains incomplete (cp. Fig. 6 *a*, *b*, and Fig. 7).

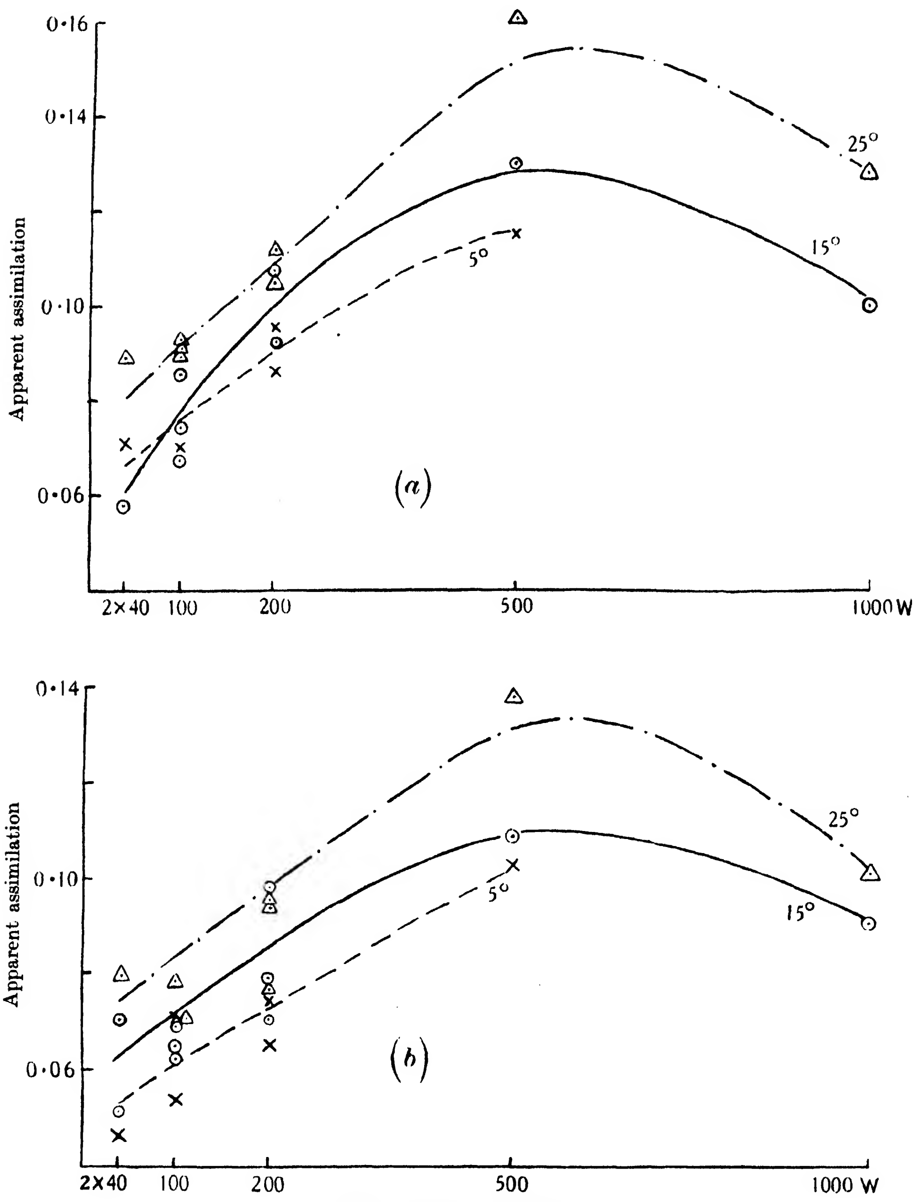


FIG. 6. Effect of changing light intensity on rate of apparent assimilation at constant temperature. (*a*) During the first 3 hours' illumination; measured as grams oxygen per litre per 100 sq. cm. (*b*) Rate after 7 hours' pre-illumination; measured as grams oxygen per litre per 100 sq. cm. liberated in 2 hours, but plotted on basis of amount which would be liberated in 3 hours, for comparison between (*a*) and (*b*).

In discussing the effect of light on assimilation, some account must be given of the kind of illumination used and of the methods adopted for comparing the different light intensities. Electric light was used because of the difficulty of obtaining uniform natural illumination at any one time, and also because with electric light, equal bilateral illumination could be obtained more easily than with daylight. Owing to the relatively large bulbs which formed the source of illumination, it was not possible to apply the inverse square law to calculate the amount of light falling on any area, even if the light at the surface of the lamp were known. Consequently the amount of light falling on the plant surface was measured photometrically by means of a Wynne "Infallible" Exposuremeter placed in the position of the plant, and was expressed as a percentage of total daylight.[1] Table II gives a comparison of the light intensities of the various lamps used at plant surface, and also the number of lumens at the lamp surface.[2] As the spectral composition of electric light is different from sunlight, it being deficient in the shorter waved blue rays, it must be emphasized that the comparison with daylight is not strictly accurate.[3] The exposuremeter can be used, however, to compare the light intensities provided by the different lamps, as they all give light of the same colour and composition.[4]

Table II. *Comparison of the light intensities of different lamps*

The values are for *one* lamp only.

Lamp used W.	Lumens at surface	Distance of lamp from plant cm.	Exposuremeter data: Time for colour change sec.	Exposuremeter data: Fraction of total daylight
40	330	15	140	1/28
100	1,160	15	60	1/12
200	2,730	20	40	1/8
500	7,920	25	15	1/3
1000	17,900	30	10	1/2

A comparison of the sources of light used by various authors, whose work is considered in more detail later on, is given in Table III (p. 132).

A study of the temperature coefficient (see Table IV (p. 132)) is interesting in connexion with the interaction of light and temperature on the assimilation of *Fucus serratus*.

[1] Total daylight (100%) was taken to be that of sunlight at noon on a bright July day, when the time taken for the exposuremeter paper, when facing north at midday (G.M.T.), to reach the darker standard tint was 5 sec.

[2] Obtained from data in the British Standards Specification, No. 161 (1934), Table II, column 31, p. 19.

[3] Cp. also Dastur & Samant (1933).

[4] As measured with an exposuremeter, about 5% of the light was lost in passing through the glass walls of the water-bath.

Table III. *Comparison of light sources of various authors*

Author	Kind of illumination	Method of measurement	Specified as:—
Kniep (1915)	"Daylight" (not direct sunlight). Assimilation chamber in air	Time for colour change on Wynne "Infallible" Exposuremeter	Time, in sec., required for colour change
Montfort (1929 *a*, *b*, 1930)	"Daylight". Assimilation chamber submerged to different depths of the sea. (Change of colour—with depth not noted)	By means of Eder-Hecht Graukeil photometer	Maximum sunlight taken as 197 units
Ehrke (1931)	(A) Electric light	—	Metre candles
	(B) Daylight. Assimilation vessels sunk to different depths of the sea. (Recognized change of colour with depth)	"Oberdorfer" photometer, strips of paper exposed for a given time, and then compared with Graukeil scale	Not stated
Lampe (1935)	(A) Daylight	—	Diffuse or sunlight
	(B) Electric light (500 W. Osram lamp)	—	Diffuse daylight (as regards assimilation influence) at its strongest intensity
M. B. Hyde (this article)	Electric light (Osram Pearl)	(*a*) By means of Wynne exposuremeter	% daylight (p. 131)
		(*b*) From data in B.S.I. Specification, No. 161 (1934)	Lumens at surface of lamp

Table IV. *Effect of temperature during the first* 3 *hours.*
Temperature coefficients (Q_{10})

Series	Light W.	Q_{10} 5–15° C.	Q_{10} 15–25° C.
II A	2 × 100	—	1·1
II B	2 × 40	—	1·1
III A	2 × 100	1·01	1·16
III B	2 × 200	1·25	1·15
IV A	2 × 100	0·95	1·13
IV B	2 × 500	1·03	1·25
V A	2 × 40	0·805	—
V B	2 × 200	1·15	—
VI A	2 × 200	—	1·33
VI B	2 × 1000	—	1·15

It is seen that the temperature coefficients are on the whole greater between 15 and 25° C. than between 5 and 15° C.

James (1934), in a theoretical consideration of assimilation, pointed out (p. 34) that three types of reaction in relation to temperature can be distinguished:

(1) Reactions which are independent of temperature, i.e. $Q_{10}=1$—includes photochemical reactions.

(2) Reactions with Q_{10} 1·2–1·5—physical processes such as diffusion.

(3) Reactions with Q_{10} 2, 3 or more—chemical reactions of the normal thermal type.

In the complex process of photosynthesis all three types of reaction are involved, and according to which one is having the greatest influence the temperature coefficient will vary. For instance, if the carbon dioxide concen-

tration is low, and the diffusion process is therefore in the foreground, the high temperature coefficients of 2 and 3 of the purely chemical part of the process will be subordinated to the lower ones of 1·2–1·5, which hold for the diffusion process. On the other hand, if the light intensity is low, the photochemical process will predominate, and Q_{10} will be unity. This has been found by Warburg (1919) ($Q_{10}=1{\cdot}06$), van den Honert (1930) ($Q_{10}=0{\cdot}9$), and is also seen in the results of my own experiments (Table IV, p. 132, Series II, III A, IV A and V A), where with lights of 2×100 W. and less, the temperature coefficient is about unity.

It can also be seen from Table IV that at very low light intensities (e.g. 2×40 W. lamps) the temperature coefficient between 5 and 15° C. is much less than unity (0·805, Series V A), i.e. there is a much greater rate of apparent assimilation at 5 than at 15° C. This relatively high rate of apparent assimilation at low temperatures and with dim light has already been discussed (p. 124), and will be alluded to again when the work of other investigators is considered. Apart from being caused by the different responses to temperature of the two processes of assimilation and respiration (one a partly photochemical and the other a more purely chemical reaction), it appears to be a characteristic feature of *F. serratus* as a species.

CORRELATION WITH THE CONDITIONS OF THE NORMAL HABITAT OF *FUCUS SERRATUS*

It has already been noted (p. 119), that Lampe (1935) correlated the reactions of *F. serratus* with seasonal variations of temperature, and Montfort (1930) also thought that this plant had a seasonal reaction to light, etc. This effect was eliminated as far as possible in my experiments by the fact that "winter" material was used throughout, the material being obtained from the shore between November and April, i.e. at a time when the sea was cold and the daylight relatively dull.

At Bexhill *F. serratus* is found abundantly throughout the year except during the late autumn and winter, when much less is present. It is in the spring, however, that the greatest amount of growth takes place. The sporelings from the gametes shed in the previous summer and autumn grow very rapidly between January and March, until by April the majority of plants are nearly full-grown, being a foot or more in length. From April onwards, but more especially after June, the plants become fertile and liberate gametes throughout the summer.[1] The plants continue to be fertile until about October, when the receptacles, and later the fronds, begin to die away, until by December they can only be seen as short, broken stipes.

[1] Contrast here Schreiber's statement (1930) that the plants of *F. serratus* round Heligoland are not fertile in June and July, but liberate gametes throughout the rest of the year. The plants at Bexhill are, however, well known to me, as my home is there.

The abundance of *F. serratus* and its active growth during the colder months of the year (January to April) may be correlated with the fact that if the light is low *F. serratus* has a greater balance of assimilation at low temperatures than at higher ones. (See my experiments, series V A, a greater rate at 5 than at 15° C.) On the other hand, if the light is bright, there is a maximum rate of assimilation at 25° C.—this approximates to the condition on the shore in summer, when the water is warm and the light bright on sunny days. My experiments with artificial light show that with bright light and high temperature there is the maximum apparent assimilation, but that there is a secondary maximum at low temperatures if the light is low. It is therefore suggested that *F. serratus* has a seasonal variation, and reacts differently to light and temperature at different times of the year. (Montfort (1930) found such a seasonal variation in *F. vesiculosus*.)

The "light place" of *Fucus serratus*

Mention has already been made in the introduction to this paper of the "light place" of littoral algae as a whole and of *F. serratus* in particular. My experiments with artificial light confirm the view of Montfort (*F. vesiculosus*, 1930) and Ehrke (*F. serratus*, 1931), that the brown algae react as sun plants in having their maximum rate of assimilation in bright light. It must be mentioned that my plants were taken (as was Montfort's *F. vesiculosus*) from a *sunny* position on the shore, and from the middle of the *F. serratus* zone, where they were exposed for about 5 hours during each tidal period, and not from near low watermark, where they would be almost continuously submerged.

To confirm the results I obtained with artificial light, I carried out some experiments outside in natural sunlight in May 1936. The sunlight was very bright (100% total daylight as determined by a Wynne exposuremeter; see p. 131). The results shown in Table V were obtained in these experiments.

Table V. *Effect of intensity of natural light on the assimilation rate of* Fucus serratus

Light intensity (% total daylight)	Temperature (° C.)	Apparent assimilation (g. O_2/l./100 sq. cm./3 hr.)
33	10	0·055
100	10	0·0804
100	20	0·104

It is seen that even at a temperature of 10° C., the rate of assimilation in full sunlight is much greater than in shade (33% total daylight), while at 20° C. in sunlight an even greater assimilation rate is obtained. This further supports the view that *F. serratus*, when growing in a sunny position on the shore, reacts as a sun plant as regards the relation of its assimilation to light.

COMPARISON WITH THE RESULTS OF OTHER WORKERS

The work of various authors on assimilation in general has already been discussed (p. 118) and the results of Kniep, Montfort, Ehrke and Lampe with marine algae have been alluded to briefly. As their work is more similar to my own than most of the work on land and freshwater plants, their results will now be considered in more detail and comparison made with my own conclusions.

Kniep (1915), working on *F. serratus* with ordinary daylight (see Table III, p. 132), found that increase in light caused an increase in the apparent assimilation rate, but that low temperatures did not depress the assimilation rate to such an extent as they did the rate of respiration, so that there was a greater *balance* of assimilation at low temperatures. Kniep therefore concluded that lowering of the temperature gave a greater excess of assimilation, which would be expected from the great abundance of brown algae in the polar seas. (Compare also Ehrke's suggested reason for the prevalence of *Fucus* in the North, mentioned on p. 136.)

Montfort (1929*a*, 1930), working on *F. vesiculosus*, and using Winkler's method, found it very difficult to draw up an assimilation curve showing the effect of light, even at the same temperature. With out-of-doors experiments in ordinary daylight he found that there was a falling off in the amount of assimilation in consecutive hours of the same afternoon—this may be due to a decrease in the light intensity.[1]

By sinking bottles to different depths in the sea to obtain synchronously higher and lower light intensities, and thus obtaining *simultaneous* readings for assimilation at different illuminations, Montfort showed that a higher light intensity gave a higher assimilation rate than a lower (see Table VI). But since the water cut off more red rays at lower depths, the results obtained were not

Table VI. *Effect of light on assimilation*—Fucus vesiculosus (*Montfort*, 1929*a*)

Light: Reading on Eder-Hecht	Light: Increase	Excess assimilation: O_2 value	Excess assimilation: Increase
L 197	21·9	3076	11·07
L 127	14·1	2568	9·24
L 100	11·1	2021	7·27
L 49	5·4	1152	4·14
L 33	3·66	850	3·06
L 9	1	278	1
L 3	0·33	−38	0

[1] Arnold (1931), however, found that the assimilation rate of *Elodea* at light intensities of more than 4000 lux fell off slowly during the day, and he attributed this mainly to fatigue. According to Arnold a 100 W. lamp at a distance of 20 cm. has an intensity of rather less than 4000 lux as measured by the Bechstein luxmeter. However, *Elodea* is considered by him as a shade plant, while Montfort regards *Fucus vesiculosus* as a sun plant.

strictly comparable, as the lights differed in spectral composition as well as in intensity.

This capacity of *F. vesiculosus* to utilize all the daylight rightly led Montfort to classify it as a sun plant. He confirmed this by showing that it responded to a change in light intensity from 1/40 to ½ of the total daylight with a 50% increase in the assimilation rate. This is comparable to the value (64%) obtained with a similar light increase by Lundegårdh (1921) for the sun plant *Nasturtium*, as opposed to an increase of 9–24% given by the shade plants *Oxalis acetosella* and *Stellaria media*.

Ehrke (1931) worked on *Fucus serratus* and used Winkler's method, but for illumination both daylight and artificial light were employed (see Table III, p. 132).

Effect of temperature. Ehrke's results with artificial light are given below (Table VII).

Table VII. *Effect of temperature on assimilation* (*Ehrke*)

Light	Rate of apparent assimilation at							
m.c.	−2° C.	5° C.	10° C.	15° C.	20° C.	25° C.	30° C.	35° C.
298	10·68	4·67	1·76	2·84	4·72	−0·96	−9·86	−21·43
2040	39·23	49·05	43·76	40·74	48·29	30·18	5·28	−22·63

In Ehrke's own curves, the *real* assimilation rate is plotted, allowance being made for respiration, which he measured at the same temperatures.[1] The rate of *apparent* assimilation is shown in this table, however, to facilitate comparison with my own results.

In both dim (298 m.c.) and brighter light (2040 m.c.), Ehrke obtained a *decrease* in the apparent assimilation rate at temperatures above 20° C. At 2040 m.c. the rate of apparent assimilation fluctuated about a mean value at temperatures from −2 to +20° C., but did not show any definite rising or falling tendency, while at temperatures above 20° C. there was a steady fall in the assimilation rate, until at 35° C. there was excess of respiration over assimilation. At a lower light intensity (298 m.c.), Ehrke found a maximum value for assimilation at −2° C., then a fall to +10° C., when the rate rose gradually with temperature until 20° C., from which point the rate fell rapidly as the temperature rose (Table VII). This should be compared with my own experiments (series V, 2 × 40 W.), where there was a greater assimilation rate at 25 than at 15° C. Ehrke's experiments at 298 m.c. had also been carried out during the spring, and the plants had been in the cold sea round Heligoland throughout the winter. Ehrke suggests that the abundance of *Fucus* in the cold and dimly lit polar seas may be due to the fact that it has a high rate of

[1] The respiration was determined at the end of a day's experiments in spring (with 2040 m.c.), and the same piece of *Fucus* was then used throughout the one temperature series. In summer, however, at 298 m.c., when new shoots were used for each temperature, the respiration was determined *simultaneously* on another shoot. Cp. p. 124.

assimilation at 0° C., if the light is low.[1] (Compare also Kniep's results quoted on p. 135.) The other maximum point for assimilation in Ehrke's experiments (+20° C.) is near the temperature of the sea in September (17° C.), when *F. serratus* is most abundant on the coasts of Heligoland.

The relation between Ehrke's temperature experiments and mine can be seen from the following table (Table VIII).

Table VIII. *Effect of temperature on assimilation*

Ehrke	M. B. Hyde
Dim light (298 m.c.). Maximum rate at −2° C. Secondary maximum at 20° C. Decrease above 20° C.	*Dim light* (2 × 40 W.). Maximum at 5° C. (series V A). Secondary maximum at 20° C. (series I and II), Fig. 1, maintained at 25° C.
—	*Medium light* (2 × 100 W.). Steady *rate* from 5 to 15° C. (rate at 5° C. sometimes higher). Maximum at 25° C. (or 30° C.). Sometimes a fall at 30° C.
—	*Brighter light* (2 × 200 W.). Steady *increase* from 5 to 25° C. Maximum at 25° C., fall at 30° C.
? *Bright light* (2040 m.c.). Secondary maximum at 5° C. Maximum at 20° C. Fall from 20 to 35° C.	*Bright light* (2 × 500 W.). Steady increase from 5 to 25° C.
—	*Very bright light* (2 × 1000 W.). Maximum at 25° C., fall at 30° C. (rate less than at 2 × 500 W.)

Both Ehrke's results and my own show a greater rate at 5 than at 15° C. with a low light intensity. This is shown in Table VII (p. 136), and also in Table IX, below.

Table IX. *Comparison of assimilation rates at 5 and 15° C., with low light intensity*

Investigator	Light	Rate of assimilation (c.c. O_2/10 g. dry wt./3 hr.) 5° C.	15° C.	Ratio 5/15° C.
Ehrke (1931)	298 m.c.	4·67	2·84	1·5/1
		Ratio of assimilation/respiration		
Lampe (1935)	Osram lamp ("weak diffuse light")	6·0 (after 1 day)	3·5 (after 1 day)	1·7/1
		6·4 (after 3 days)	4·4 (after 3 days)	1·4/1
		g. O_2/l./100 sq. cm./3 hr.		
M. B. Hyde (1936)	2 × 40 W.	0·074	0·060	1·25/1

The contrast between Ehrke's experiments and mine is the lower temperature of maximum assimilation in Ehrke's experiments (20° C.) as compared with 25 or 30° C. in my experiments.

[1] Harder (1915), studying the assimilation of *F. serratus*, and working with weak artificial light (100 m.c., 65 cm. away) found that the rate of apparent assimilation (as measured by O_2 output) was twenty times as much at 0° C. as at 20° C., thus supplying further support for this view. Lampe (1935) records a similar greater rate of assimilation at 5 than at 15° C. for *F. serratus*.

Effect of light. In natural daylight Ehrke found that the apparent assimilation rate fell off steadily with increasing depth of the sea (i.e. with increasing light intensity). The following table (Table X), taken from Montfort's paper (1930), shows the relation between his results and those of Ehrke.

Table X. *Comparison of results of Ehrke and Montfort*

Depth (m.)	Montfort (Bergen, Sept. 1927) *F. vesiculosus*	Ehrke (Heligoland, Aug. 1929) *F. serratus*
1	—	100
1·7	100	—
4	—	*ca.* 70
8	—	*ca.* 24
10·5	52	0
16	—	0
20	7	—

Although from the table it appears that *F. vesiculosus* is able to assimilate at greater depths than *F. serratus*, the relative light intensities at comparable depths (known to be very variable) are not specified, and it may be that at Bergen there was as much, or more, light at 20 m. as there was at 10 m. depth off Heligoland.[1]

With artificial light, Ehrke found (at temperature 10° C.) a progressive increase in apparent assimilation with increasing illumination. This is seen in Table XI.

Table XI. *Effect of light intensity on assimilation* (*Ehrke*)

Light (m.c.)	100	200	400	800	1600	3200
Apparent assimilation (c.c. O_2)	−7·49	−4·79	4·34	18·42	33·04	49·41

This steady increase in the rate of apparent assimilation with increase of light intensity, so that the maximum value is not reached at over 3000 m.c., is in striking agreement with my results with artificial light up to 2 × 500 W. (believed to be much more than 4000 m.c. in intensity), although by working with still stronger lights (2 × 1000 W.)—far brighter than those used by Ehrke—I found an ultimate fall in the assimilation rate.

The work of Lampe (1935) on the assimilation of *F. serratus* will be considered briefly, because he seems to have been the only other investigator of this alga who considered the possibility of a falling off in the assimilation rate during the course of a day's experiments.

Working with the light intensity of a 500 W. Osram lamp, he exposed "winter" plants of *F. serratus*, taken from the sea (temperature 5° C.), to temperatures of 5, 15 and 21° C., giving them alternate hours of light and darkness. (In the latter periods the respiration rate was measured.) The assimilation rate was thus determined in the first, third, fifth and seventh hours of exposure to the experimental temperature, and showed no falling off

[1] The amount of suspended matter is of great significance.

with time at any of the three temperatures used. His results are shown in Table XII. They are not strictly comparable with mine because in Lampe's experiments an hour of illumination alternated with an hour of darkness. These dark periods would tend to dispel any possible effect of solarization, and although the highest temperature used (21° C.), was much higher than the temperature of 5° C. to which the plants were accustomed, I do not think it was high enough to have any injurious effect.

Table XII. *Effect of temperature on the assimilation of* Fucus serratus *throughout the day, with "medium" light (Lampe)*

	Excess assimilation at		
Rate in	5° C.	15° C.	21° C.
First hour	329	530	564
Third hour	335	552	556
Fifth hour	313	560	537
Seventh hour	334	564	570

The results agree with mine in showing that with medium light the rate of assimilation can be maintained for a number of hours. I found that at 2 × 100 W. illumination, the rate, after the first hour, remained constant at 15 and 20° C. for at least 8 hours, and although at 5° C. my experiments showed a slight fall in the assimilation rate during the day, I attributed this to the fact that my plants had been growing at 10° C. and so had become accustomed to this temperature, while the temperature of the habitat of Lampe's plants was 5° C., so that this as an experimental temperature would have no retarding effect.

Lampe also found that although in bright sunlight the rate of apparent assimilation was greater at 15 and 21 than at 5° C., with weak diffuse light there was a much greater balance of assimilation at 5° C. than at the higher temperatures (see Table VIII, p. 137). This is in agreement with my work at 2 × 40 W., as well as supporting the results of Kniep (1915), Harder (1915), and Ehrke (1931), and again suggests the suitability of *F. serratus* as a plant of arctic seas, where light and temperature are both low.

Tables XIII and XIV (p. 140) summarize my results, each series representing the experiments carried out (usually on consecutive days) with the same piece of thallus at the same light intensity but at different temperatures (5, 10, 15 and 20° C.). The same piece however was not used for both 25 and 30° C. in order to avoid any harmful effect of these somewhat high temperatures.

In Table XIV are shown the values for each light and temperature, averaged from the values set out in Table XIII. These values were used in constructing the model (Fig. 7) and are represented to scale at the lines of intersection of the perpendicular strips of cardboard. These strips are set upon a base on which are shown the abscissae representing temperatures and the ordinates representing intensity of illumination.

Table XIII. *Rate of apparent assimilation during first 3 hours*

Calculated as g. oxygen per l. per 100 sq. cm. per 3 hr.

Date	Series	Light W.	Temperature 5° C.	10° C.	15° C.	20° C.	25° C.	30° C.
Nov.–Dec. 1935	II A	2 × 100	—	—	0·0859	0·0921	0·0894	0·0957
	II B	2 × 40	—	—	0·0915	0·0948	0·1003	0·1026
Jan.–Feb. 1936	III A	2 × 100	0·0713	0·0782	0·0705	0·0823	0·0888	0·0802
	III B	2 × 200	0·0869	0·0835	0·0935	0·1008	0·1069	0·0926
Feb. 1936	IV A	2 × 100	0·0794	—	0·0763	—	0·0917	—
	IV B	2 × 500	0·1185	—	0·1288	—	0·1610	—
Mar. 1936	V A	2 × 40	0·0735	—	0·0590	—	—	—
	V B	2 × 200	0·0963	—	0·1082	—	—	—
June 1936	VI A	2 × 200	—	—	0·0847	—	0·1127	0·0888
	VI B	2 × 1000	—	—	0·1030	—	0·1280	0·0662
June 1937	VII A	2 × 1000	0·0540	—	—	—	—	0·07806
	VII B	2 × 100	0·05169	—	—	—	—	0·07300
June 1937	VII B_2	2 × 500	—	—	—	—	—	0·06615

Table XIV. *Rate of apparent assimilation during the first 3 hours*

Average values for different temperatures and light intensities

Light (W.)	Temperature 5° C.	10° C.	15° C.	20° C.	25° C.	30° C.	Time of year
2 × 40	0·0735	0·0720	0·0700	0·0848	0·0900	0·0926	Nov.–Dec. 1935 Mar. 1936
2 × 100	0·0753	0·0782	0·0776	0·0871	0·0900	0·0880	Nov. 1935–Feb. 1936
	0·0517	—	—	—	—	0·0730	June 1937*
2 × 200	0·0860	0·0835	0·0955	0·1008	0·1098	0·0907	Jan.–Mar. 1936
2 × 500	0·1185	—	0·1288	—	0·1610	—	Feb. 1936
	—	—	—	—	—	0·06615	June 1937*
2 × 1000	—	—	0·1030	—	0·1280	0·0662	June 1936
	0·0540	—	—	—	—	0·0781	June 1937*

* These values were kindly found for the author by Miss B. Duthy, B.Sc., and Miss E. Robson, working in the same laboratory and following the same method using material from the same source similarly handled.

It will be seen that the highest values of carbon assimilation are obtained at 2 × 500 W. (equivalent to about 2/3 total daylight), and in this respect *F. serratus* is a sun plant (cf. Montfort, 1929 *a*), as contrasted with a typical shade plant, which gives no increase of assimilation with light brighter than 1/10th of total daylight (Lundegårdh, 1921). With light of 2 × 1000 W., however, the assimilation values were about 30% lower than that found previously for a similar piece of *Fucus* at 500 W. *F. serratus*, therefore, differs from a typical sun plant in that bright daylight cannot be fully utilized and may even have a depressant effect on the rate of assimilation in *sea water*. On the shore it is only at low water or during exposure that *Fucus* is subject to full sunlight, as when submerged a considerable amount of light is cut off by the water. The reduced rate of assimilation which in this series of experiments has been shown to occur at high light intensities might therefore reasonably be expected from a plant growing in this environment, the habitat being alternately that of a sun and shade plant.

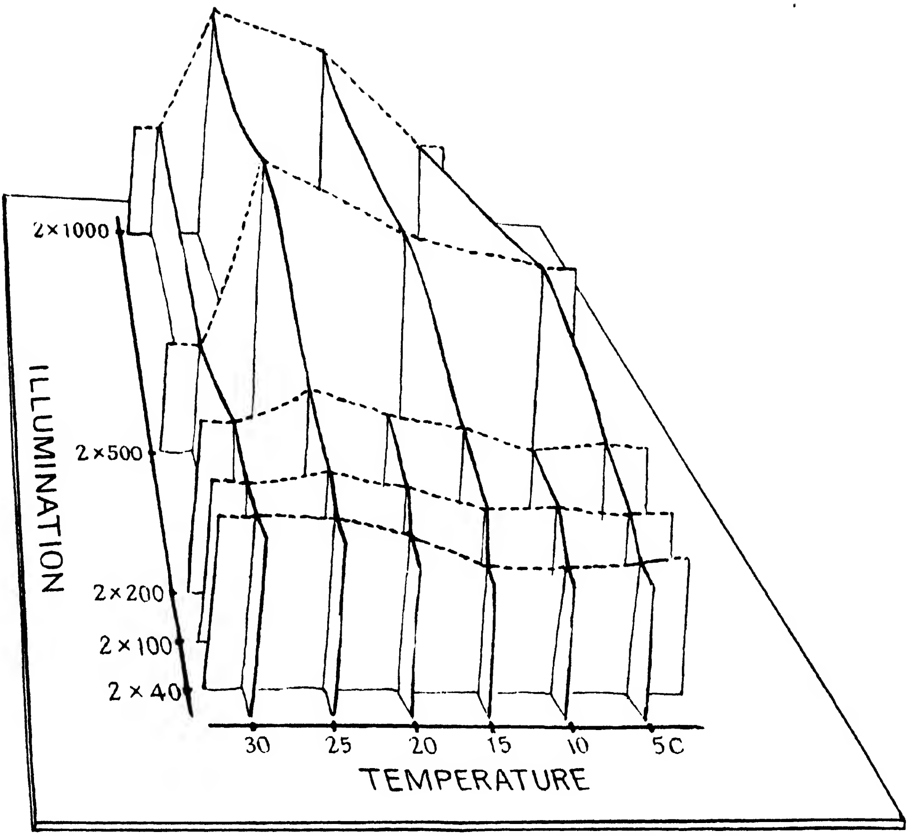


FIG. 7. Drawing of paper model showing combined effects of light and temperature on rate of apparent assimilation of *Fucus serratus*. The model is shown as viewed from above on the left, involving considerable foreshortening. The values of the apparent assimilation are represented by the heights at the points of intersection of the vertical partitions.

CONCLUSIONS

Effect of temperature. 1. When light is not limiting (i.e. using 2 × 200 W. lamps), the rate of apparent assimilation of submerged fronds of *Fucus serratus* increases with rising temperature to a maximum value at 25° C. (series III), or 30° C. (series II), after which there is a fall in the apparent assimilation rate (Graphs, Fig. 3, p. 127). With 2 × 500 W. lamps, during the first 3 hours, the increase in rate from 15 to 25° C. is greater than from 5 to 15° C. (Graphs, Fig. 5, p. 129), the temperature coefficient from 5 to 15° C. being 1·03, while that from 15 to 25° C. is 1·25 (Table IV, p. 132, series IV B).

2. If the light intensity is low, the higher temperatures do not have such an accelerating effect, the maximum apparent assimilation rate being at 5° C., with a secondary maximum at 25° C. The latter rate is maintained but not exceeded at 25° C. (Graphs, Fig. 5, p. 129).

Effect of light. 1. Increase in light intensity from 660 to 15,840 lumens causes a progressive increase in the apparent assimilation rate of *F. serratus* at any one temperature (Graphs, Fig. 6 *a*, *b*). This increase is greatest in the first 3 hours, being then about double the increase seen after 7 hours' pre-illumination (see also Table I, p. 128).

2. Owing to the accelerating effect of high temperatures, for any one light series, the rate is greater at high temperatures than at low ones; for example, in Fig. 6, temperature is limiting below 25° C. at bright light, and the full light effect is only evident at 25° C.

3. The capacity of *F. serratus* still to show a rising assimilation curve with increase of light intensity up to the equivalent of 2/3 total daylight (16,000 lumens) causes it to be classed as a sun plant.

4. The results which led to the above conclusions have been expressed in the form of a model, see p. 141.

In conclusion the writer wishes to express her best thanks to Dr E. M. Delf, F.L.S., of Westfield College (University of London), for her stimulating criticism and encouragement during this investigation and also to Mr Percy J. Smith for much help with the drawing of Fig. 7.

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STUDIES IN SALT-MARSH ECOLOGY
SECTIONS I TO III

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(*With eighteen Figures in the Text*)

CONTENTS

I. Physiography and the environmental factors

Introduction

From time to time the principal salt marsh areas of England have been subject to investigation, and a considerable body of information has been collected in connexion with the analysis of the environmental factors. The collection of such data occupies much time and, in general, each investigation has been essentially a study of one or two particular factors (Steiner, 1934; Wiehe, 1935). Many of these studies have concerned themselves with relatively small marsh areas, since these present an apparently easier problem. Small marshes, however, are very often formed as a result of a shingle bar enclosing a small area, leaving only a narrow outlet. These "closed" marshes characteristically develop much more rapidly than large "open" marshes, and in any study of

such small marshes this rapid development and consequent compression of the developmental phases must be borne in mind.

There are at least ten major factors of the environment which may operate on any salt-marsh area. Few of these factors act wholly independently of the others, and hence an ideal study of a salt marsh would have to include a consideration of them all, but the time available for collecting data is usually limited. Any study that concerns itself with one or two factors must be interpreted with caution in the light of possible interference from any of the other unknown factors. The ideal ecological study should also include a detailed investigation of the habits and requirements of the dominant species; in other words, it demands a series of autecological studies. Such studies will undoubtedly be facilitated by a quantitative knowledge of the environmental factors. This information should permit the devising and carrying out of a series of field and laboratory experiments, designed to indicate exactly how far each factor is responsible for the behaviour and distribution of the individual species. Very few experiments of this nature have as yet been recorded in the literature. A few preliminary attempts have been made in this direction during the present investigation, but again it has not proved possible to collect adequate data about *all* the important environmental factors.

The English salt marshes are usually characterized by the presence of both phanerogams and algae, the latter often in great abundance. This is in distinct contrast to the salt marshes of America (Johnson & York, 1915; Steiner, 1934) where the algae play an insignificant role. The marshes of Blakeney (Oliver, 1925–9), Holme (Marsh, 1915; Conway, 1933), Scolt Head (Chapman, 1934), the Dovey (Yapp *et al.* 1917), and the River Nith (Morss, 1927), have been studied in respect of the phanerogams, whilst papers have appeared concerning the algal vegetation of the Blakeney Point (Baker & Blandford, 1912, 1916), Clare Island (Cotton, 1912), Lough Ine (Rees, 1935), Canvey and Dovey (Carter, 1934–5) marshes. In the present investigation a study has been made of both the algal and phanerogamic vegetation of Scolt Head Island in Norfolk, and an attempt has been made to secure a general picture of the series of marshes between King's Lynn and Blakeney. This is because the present author is convinced that the marshes extending from the Wash to the Thames form an entity within what may be termed the Salt Marsh Formation of North Europe. It is probable that these east coast marshes exist under somewhat different conditions to those along the English Channel and the west coasts of England and Ireland.

Physiography

The marshes between Hunstanton and Blakeney have nearly all been built up behind shingle bars laid down on a wide sandy foreshore (Steers, 1934). In places one can detect a succession of bars seawards, although many of the older ones have been obscured by the "inning" of the marshes. A diagrammatic

picture of this general physiographic structure is seen in Fig. 1. The oldest marshes are usually no longer wild and have been reclaimed for pasture land. When a geological investigation of the marshes was undertaken (Steers, 1934), it was found that the oldest landward marshes near the ancient sea cliff had a considerable depth of mud, whilst on the middle-aged and young marshes the mud was generally shallow. This difference can probably be explained if the

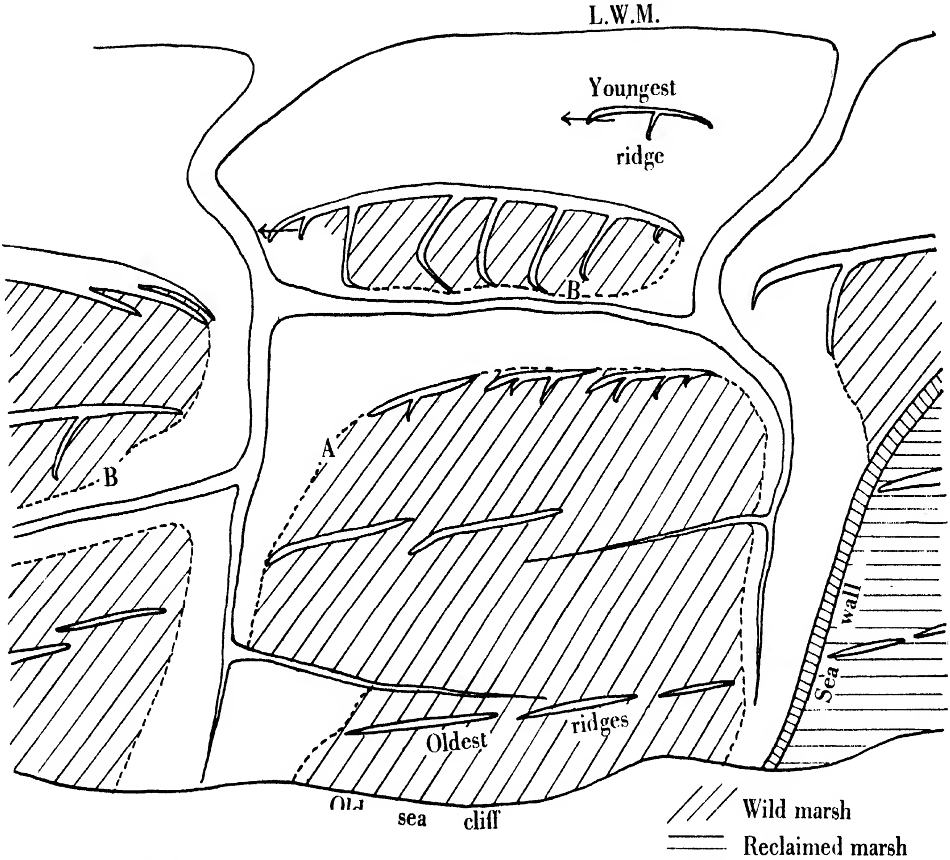


FIG. 1. Diagrammatic scheme of the physiography of the North Norfolk marshes. Arrows indicate direction of shingle growth caused by wave action. Growth of marsh—A, seaward; B, landward—protected by outer seaward ridges.

two chief methods of salt marsh formation are briefly considered. Two alternative conditions of salt marsh formation may be distinguished:

(1) Marshes are formed during a gradual subsidence of the land. These marshes either possess a deep layer of silt or of peat, as in the New England marshes of N. America where one may frequently find a depth of 20 ft. of peat. The silting or organic accretion must take place at a greater rate than that at which subsidence proceeds or else no true salt marsh will ever be

formed (Richards, 1934; Nielson, 1935). The great depth of mud (13 ft. +) on the old marshes near Brancaster Staithe suggests that they were formed during a period of coastal subsidence. The presence of peat beds at three different levels on the foreshore is evidence that subsidence has actually occurred in the past.

(2) Marsh formation takes place through the silting up of lagoons or areas protected by sand or shingle bars, without any accompanying land movement. The rise in level may be due to the deposition of silt or to the accumulation of plant remains, but in either case the thickness of the deposit will not be great, and will be less than the maximum tidal range (Nielson, 1935). The shallow soil depth of the younger Norfolk marshes suggests very strongly that they have developed along these lines during a period of coastal stability.

It seems probable, therefore, that both types of salt marsh formation are represented in the Norfolk marshes. The actual process of development has been described in detail elsewhere (Steers, 1934) and hence need not be repeated here. One feature to which attention is worth calling is the gradation from salt marsh to fresh-water marsh which can be seen at Thornham and Brancaster. Such transitions are common on the eastern coast of North America, but this appears to be the first time that it has been recorded for the east coast marshes of England.[1] The relative lack of these transitions may be ascribed to the practice of enclosing ("inning") the older marshes.

The environmental factors

So far as the appearance and disappearance of most of the algal and phanerogamic communities are concerned, it is probable that the tides must be regarded as the major factor. These control the vertical distribution of many of the species, operating at high levels through the number of submergences and at low levels through the number of exposures. The subterranean aeration of the soil must also play a considerable part in determining the presence of some of the phanerogams. The horizontal distribution of the species at any given level may be regarded as under the principal control of drainage and salinity, although it is probable that certain species are controlled by other factors. It seems, therefore, that the most satisfactory results should be obtained by a detailed study of these primary factors, and the subsequent application of the knowledge so gained to an autecological investigation of the dominant species. The principal interacting factors on the Norfolk marshes appear to be the following (cf. also Nichol, 1935):

(1) *Tides.*	(3) *Drainage.*	(5) *Water-table.*
(2) *Salinity.*	(4) *Aeration.*	(6) *Rainfall.*

(7) *Soil.* The principal feature in the soil of these marshes is the high percentage of silt and clay. Their composition throws considerable light on

[1] A similar transition is said to occur on some Scottish marshes in the Firth of Forth.

the behaviour of the water movements and aeration, and it emphasizes further the difference between these marshes and those of New England and Ireland, where the soil is a loose spongy peat. Table I gives typical analyses of soils from different marshes on Scolt Head Island.

Table I

	Marsh of medium height					Low marsh		High marsh
Soil type	Shingle %	Sandy mud %	Silty surface mud %	Surface mud—creek edge %	Clay mud %	Surface mud %	Sand %	Surface mud %
(*a*) Soil not passing 3 mm. sieve	55·55	0·05	0·58	0·00	0·00	0·00	0·00	4·85
(*b*) Soil not passing 2 mm. sieve	1·34	0·00	0·00	0·00	0·00	0·00	0·00	0·32
(*c*) Soil not passing 1 mm. sieve	2·19	0·08	0·19	0·00	0·00	0·00	0·90	0·00
(*d*) Soil not passing 0·5 mm. sieve	2·78	0·92	0·58	0·00	0·00	0·38	1·37	1·94
(*e*) Soil passing 0·5 mm. sieve	38·13	98·95	98·65	100·00	100·00	99·51	98·54	92·87
Roots	0·00	0·05	0·58	0·00	0·00	0·00	0·00	4·85
Stones	55·55	0·00	0·00	0·00	0·00	0·00	0·00	0·00
(Fraction *e*)								
Coarse sand	64·88	56·96	0·95	0·30	2·23	0·55	63·63	35·79
Fine sand	11·00	13·76	12·42	16·85	18·66	9·03	11·97	5·29
Clay	11·76	13·42	37·71	31·42	35·05	33·88	8·68	15·20
Silt	8·49	9·95	28·87	24·20	28·67	31·52	7·11	10·93
Carbonate	0·00	0·00	0·53	7·22	1·92	3·44	2·07	0·00
Moisture content	1·14	1·37	4·44	2·72	4·12	5·24	0·91	5·56
Humus	2·77	3·31	10·09	8·91	8·77	13·58	2·72	19·10
Total	100·04	98·77	95·01	91·62	99·42	99·24	97·09	91·87

(8) *Evaporation.* This factor is principally of importance in controlling the distribution of the algae. Throughout the summer evaporation takes place at such a rate that salt crystallizes out on the soil surface and upon the algae. Many algae will, however, occur in shaded areas at levels far above those at which they can no longer exist on the exposed open marsh.

(9) *Temperature.* Setchell (1920) has demonstrated that the occurrence of *Zostera marina* is associated with the temperature changes of sea water. It is doubtful whether this factor is important in controlling the distribution of the plants actually living on the salt marshes, but it may be significant in controlling the distribution of some of the algae, and possibly also *Zostera nana* and *Ruppia maritima*.

(10) *Biota.* This concerns the interrelations of the phanerogams, algae and animals.

II. THE TIDES

It has been stressed in the previous section that the tide is the major factor of the environment. Before considering how the tides may influence the distribution of the vegetation, it is necessary to know something of tidal behaviour at different marsh levels, selecting, in particular, those levels which are related to plant distribution.

Technique

The methods by which the results were obtained have been described in detail in the recent handbook on Scolt Head Island,[1] and need not be repeated here. The levels used in this investigation are all referred to an arbitrary datum, Island Zero Level (I.Z.L.) which is +7·0 ft. O.D. The features investigated were (A)[2] number of submergences per annum, (B, C) periods of greatest submergence, (D, E, F) maximum period of non-tidal exposure (one or more days during which no tide covers the marsh), (G) hours of submergence each month, and (H, I, J) hours of submergence in daylight. Daylight was taken as commencing one hour before sunrise and ending one hour after sunset. This may not be entirely justifiable but it forms a convenient standard. A summary of all these features is set out in Table II. It is not proposed to elaborate this further because a study of the table itself will be the most convenient means of understanding the conditions existing at the different levels.

Table II is more elaborate than one published previously (Chapman, 1934, p. 125), because more data have been available upon which the calculations could be based: hence it will be found that there are slight differences from the earlier table. When the first table was published, however, it was emphasized that the results for the hours of submergence each month were compiled from tidal charts for only 10 weeks, whereas the figures in Table II were obtained from charts for 19 weeks. There was also a wider choice of suitable periods for the purpose of calculating the hours of submergence in daylight, so that these figures also differ slightly.

Submergence per annum

A detailed study of Table II indicates that the marshes above and below a level of +1·10 ft. I.Z.L. exist under very different conditions, and the plants on these marshes will be subject to the same differences. In an earlier paper the delimiting level was placed at +1·30 ft. I.Z.L., but with the fuller information now available it is clear that 1·10 ft. is the more correct figure. The fundamental differences are set out in Table III.

[1] **Chapman, V. J.** in STEERS, *Scolt Head Island.* The Ecology. Cambridge, 1934.
[2] See Table II.

Table II

	A	B	C	D	E	F	G	H	I	J
Level ft. above I.Z.L.	No. of submergences per annum	Periods of greatest submergence	Month with maximum number of submergences	Maximum period of non-tidal exposure days	Month with maximum period of non-tidal exposure	Average no. of hr. submerged per month	Submergence / Emergence hr./month	Average hr. of submergence in daylight	Submergence / Emergence hr. in daylight	Period with maximum submergence in daylight
3·36	82	Ap., May, Sept., Oct.	16 Sept., Oct.	57	June–Aug.	3·0	0·004	0·06	0·004	Sept.
3·11	104	Ap., Sept.–Nov.	16 Sept.–Nov.	37	Dec.–Jan.	6·9	0·009	0·10	0·007	Sept.
2·79	166	Mar., Oct.	24 Oct.	25	June–July	10·5	0·014	0·35	0·025	Sept.
2·52	200	Mar., Ap., Sept.–Oct.	24 Sept., Oct.	25	June–July	21·2	0·029	0·50	0·029	Sept.
2·24	214	Feb.–Ap., Oct.	26 Oct.	24	June–July	26·3	0·037	0·65	0·048	June
2·02	234	Mar.–Ap., Oct., Nov.	26 Oct., Nov.	22	June–July	30·1	0·043	0·70	0·051	June
1·85	258	Mar.–Ap., Oct.	30 Oct.	22	June–July	36·3	0·052	0·75	0·055	June
1·67	290	Mar., Oct.	34 Oct.	22	June–July	43·2	0·063	0·90	0·067	June
1·34	338	Mar., Sept.–Oct.	36 Sept.–Oct.	22	June–July	56·8	0·084	1·05	0·079	June
1·23	344	Jan., Mar.–Ap., Aug.–Oct.	36 Oct.	22	June–July	57·5	0·086	1·2	0·092	June
1·09	362	Oct.	36 Oct.	10	Jan., May–June	70·0	0·106	1·2	0·092	June
1·04	372	Jan., July, Oct.	36 Oct.	8	Feb.–Ap.	70·0	0·106	1·2	0·092	June
0·88	383	Jan., Ap., July, Oct.	38 Oct.	8	Feb.–Ap.	80·3	0·121	1·4	0·108	June
0·38	431	Jan.–Mar., Oct., Nov., Dec.	40 Oct.	8	Feb.	105·4	0·165	1·8	0·144	June
0·10	466	Jan., Mar., July, Oct., Nov., Dec.	40 Oct.	7	March	119·8	0·192	2·1	0·172	June
−0·18	497	Jan., July, Oct., Nov.	44 Jan., July, Oct., Nov.	6	March	127·4	0·211	2·3	0·192	June
−0·55	567	Jan., May, July, Nov., Dec.	52 July	5	Feb., Mar., Ap., May, Sept.	147·9	0·253	2·7	0·232	June
−0·90	582	Jan., July, Oct., Dec.	54 July	5	Feb., Mar., Ap., May	171·1	0·305	3·0	0·265	June
−1·18	612	June, July, Oct., Dec.	56 Dec.	5	March	179·3	0·317	3·3	0·300	June
−1·55	640	Jan., June, July, Dec.	58 July, Dec.	5	March	200·3	0·377	3·8	0·362	June
−1·88	665	Jan., June, July, Dec.	60 Jan., July, Dec.	3	Feb., Mar., Ap., Oct.	216·5	0·411	4·0	0·388	June
−2·19	681	Jan., July, Aug., Dec.	60 Jan., July, Aug., Dec.	3	Mar., Ap.	240·9	0·479	4·2	0·416	June
−2·89	703	Jan., Mar., May, July, Aug., Oct., Dec.	60 Jan., Mar., May, July, Aug., Oct., Dec.	1	March	275·2	0·603	5·0	0·538	June
−3·25	705	Jan., Mar., May, July, Aug., Oct., Dec.	60 Jan., Mar., May, July, Aug., Oct., Dec.	None	—	286·1	0·641	5·2	0·599	June
−4·65	705	Jan., Mar., May, July, Aug., Oct., Dec.	60 Jan., Mar., May, July, Aug., Oct., Dec.	None	—	348·5	0·881	7·0	0·959	June

Table III

	Periods of maximum submergence
Upper marshes (above +1·10 ft. I.Z.L.)	(*a*) March–May (*b*) September–October
Lower marshes (below +1·10 ft. I.Z.L.)	(*a*) December–January (*b*) April–May (*c*) July (*d*) October

It is important to realize that on the upper marshes the periods of most frequent submergence occur:

(*a*) At the spring equinox, when the seedlings are just coming up. I have obtained some evidence which suggests that the density of certain species on the New England marshes may be determined by these spring floodings. Wiehe (1935) has also shown that the density of *Salicornia europaea* on the Dovey marshes is largely dependent upon the degree of flooding by the spring tides.

(*b*) At the autumn equinox in the fruiting season. Since the spread of many of the marsh plants is dependent upon the seeds being carried by the tide, the agent of dispersal is present at the critical period.

The rejuvenation of the desiccated marsh algae must also be secured by these tides and therefore the spring equinox series will be of the utmost importance in perpetuating the algal species. Between these two periods there is a long period of non-tidal exposure in the summer (two or more days during which no tide covers the marsh) when considerable desiccation occurs. The whitened remains of algae strew the ground, but some filaments remain alive through being buried in the soil or under the dead plants until the incidence of the autumn tides restores them to vigorous growth. This long summer exposure probably plays a fundamental part in limiting the upper boundaries of some species.

The relation of the phanerogams to submergence has been discussed elsewhere (Chapman, 1934), whilst the relationship of the algal species is shown in Fig. 2. It will be seen that fifteen species occur almost wholly on the upper marshes. Of these, nine are Cyanophyceae, a group which is particularly adapted to tolerate adverse conditions. Two species belong to the Phaeophyceae, one being a marsh Fucoid (*Fucus vesiculosus* ecad. *muscoides*), whilst the other (*Phaeococcus adnatus*) is a microscopic soil form, which is sparse during the summer and attains its maximum abundance in the winter. The decrease of this species in summer may be correlated either with the long summer exposure or else with the salt encrustation (high salinity). The remaining four species are Chlorophyceae, of which *Vaucheria sphaerospora* can be regarded as a terrestrial species. *Endoderma perforans* is found principally in colonies of *Rivularia atra* which serve as a protection against desiccation. Some evidence has been accumulated which suggests that *Enteromorpha clathrata* f. *prostrata*

is a form developed purely as a response to conditions of exposure. It is worth noting that no species of Cyanophyceae is confined wholly to the lower marshes: their relative infrequency here is probably connected with competition or

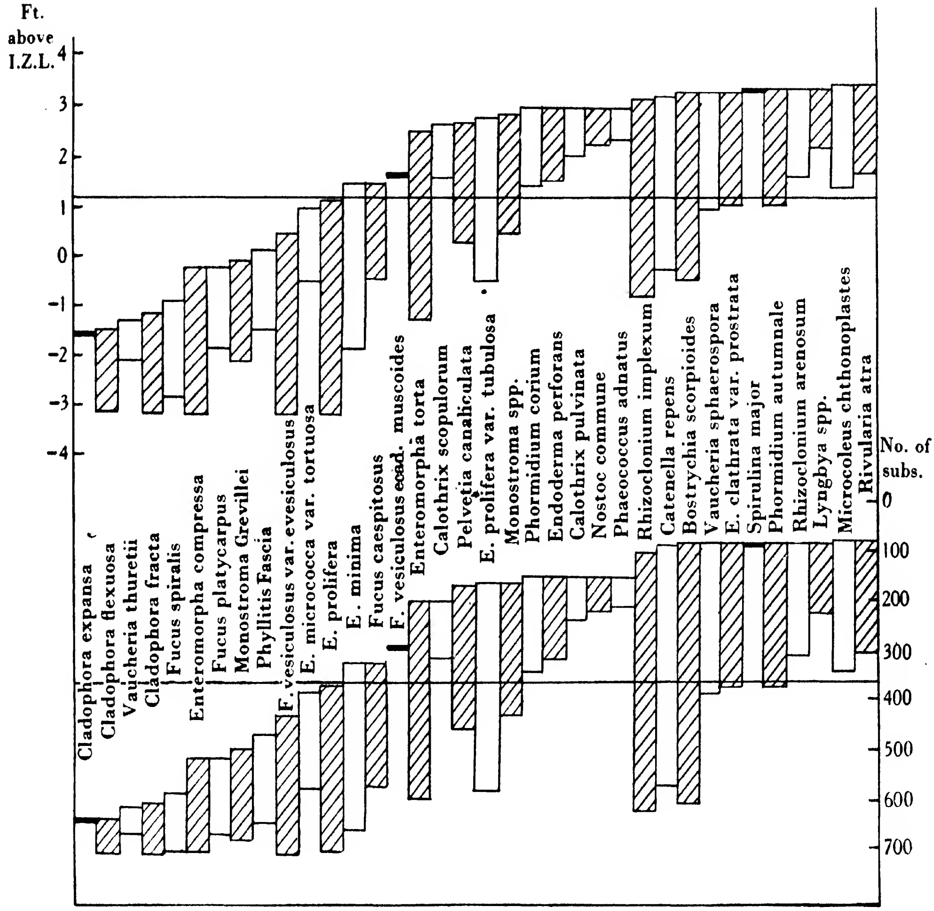


FIG. 2. Algal species growing on the salt marshes of Scolt Island. Ranges and number of submergences *per annum*. Upper marshes above + 1·10 ft. I.Z.L.

failure of the reproductive elements to secure a foothold. Fig. 3 represents the ranges and number of annual submergences of thirteen communities of algae.

On the lower marshes it can be seen that there is a period of maximum submergence during the summer, in contrast to the long exposure on the upper marshes. Plants on these marshes, therefore, are not subject to the same degree of desiccation as those on the upper marshes. In a study of the salt marshes of New England I have found that there is a similar separation into

upper and lower marshes, each having their own set of conditions, so that this feature is not an isolated phenomenon confined to the Norfolk marshes.

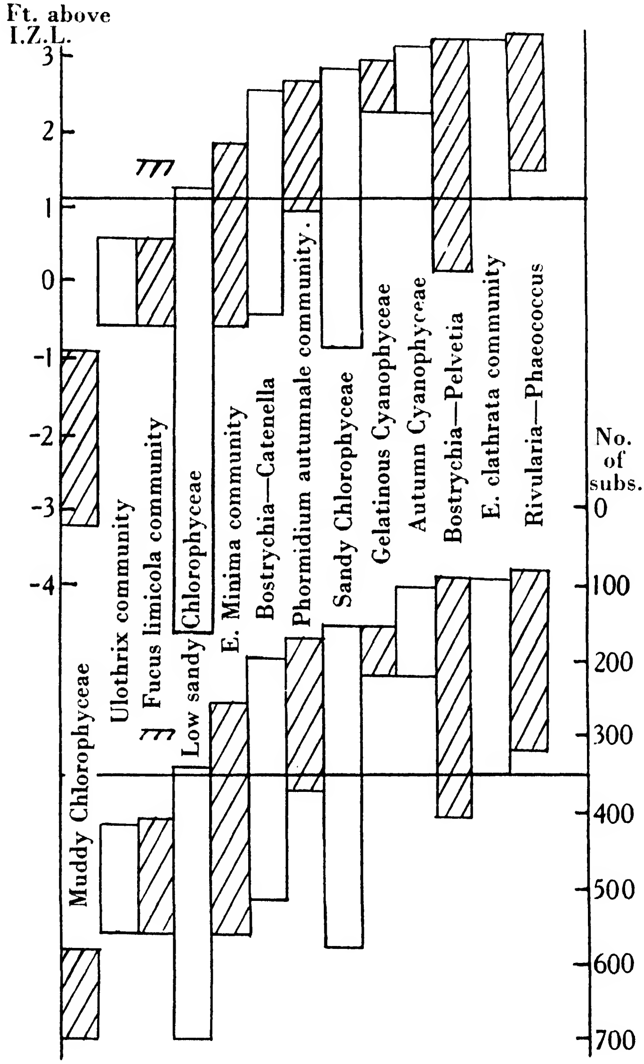


Fig. 3. Ranges and number of annual submergences of the salt marsh algal communities on Scolt Island.

Periods of non-tidal exposure

The duration and number of non-tidal exposures are an important feature of the marshes, because they provide a clue to the degree of desiccation which each species may undergo. Fig. 4 shows typical exposure charts calculated

for the upper and lower limits of six phanerogamic species. The non-tidal exposures of thirty-six algal and eighteen phanerogamic species have been calculated. When the diagrams were drawn they were all found to be similar *to one or other of those in Fig. 4. At the high levels the long continuous summer exposure is very evident.*

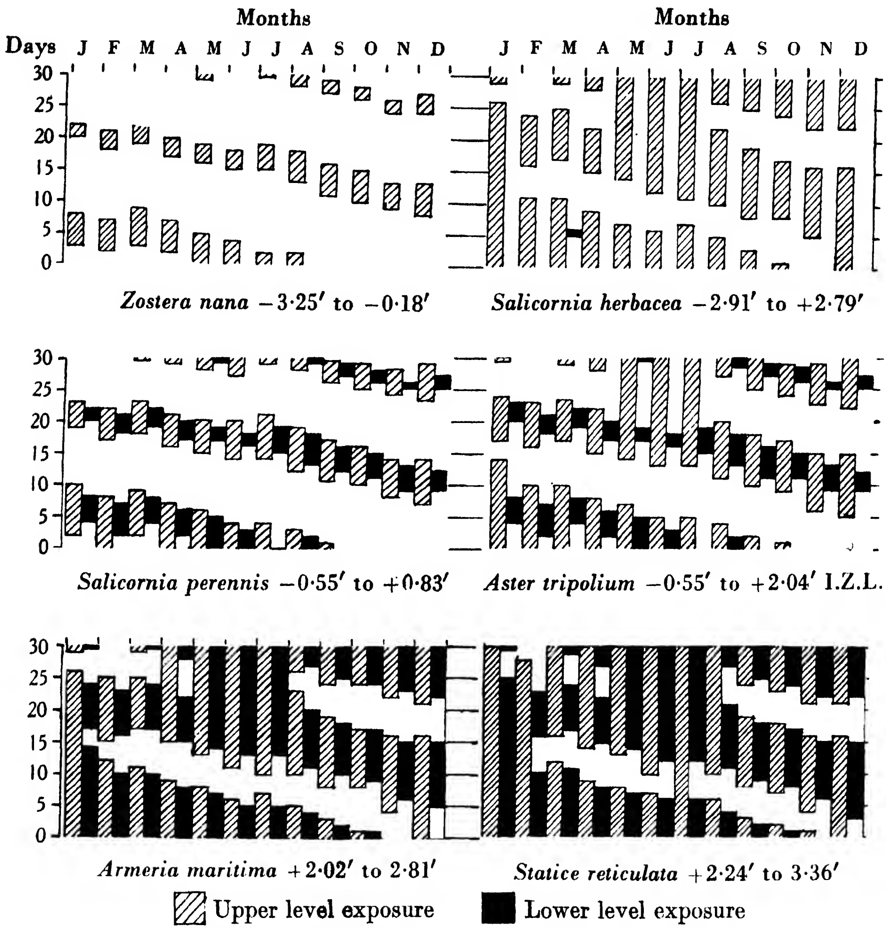


FIG. 4. Charts indicating characteristic features of non-tidal exposure for salt marsh plants at the limits of their vertical range.

Hours of submergence and exposure

A study of the results in this section indicates that the flowering plants do not descend below mean sea-level in this area. The lowest limit for any phanerogam is that for *Zostera nana* (−3·25 ft. I.Z.L.), where it is submerged on an average of 9·26 hr. per diem. If the temperature of the water plays any

part in determining its flowering period, then the hours of inundation may be of considerable significance. Another feature of interest is that none of the

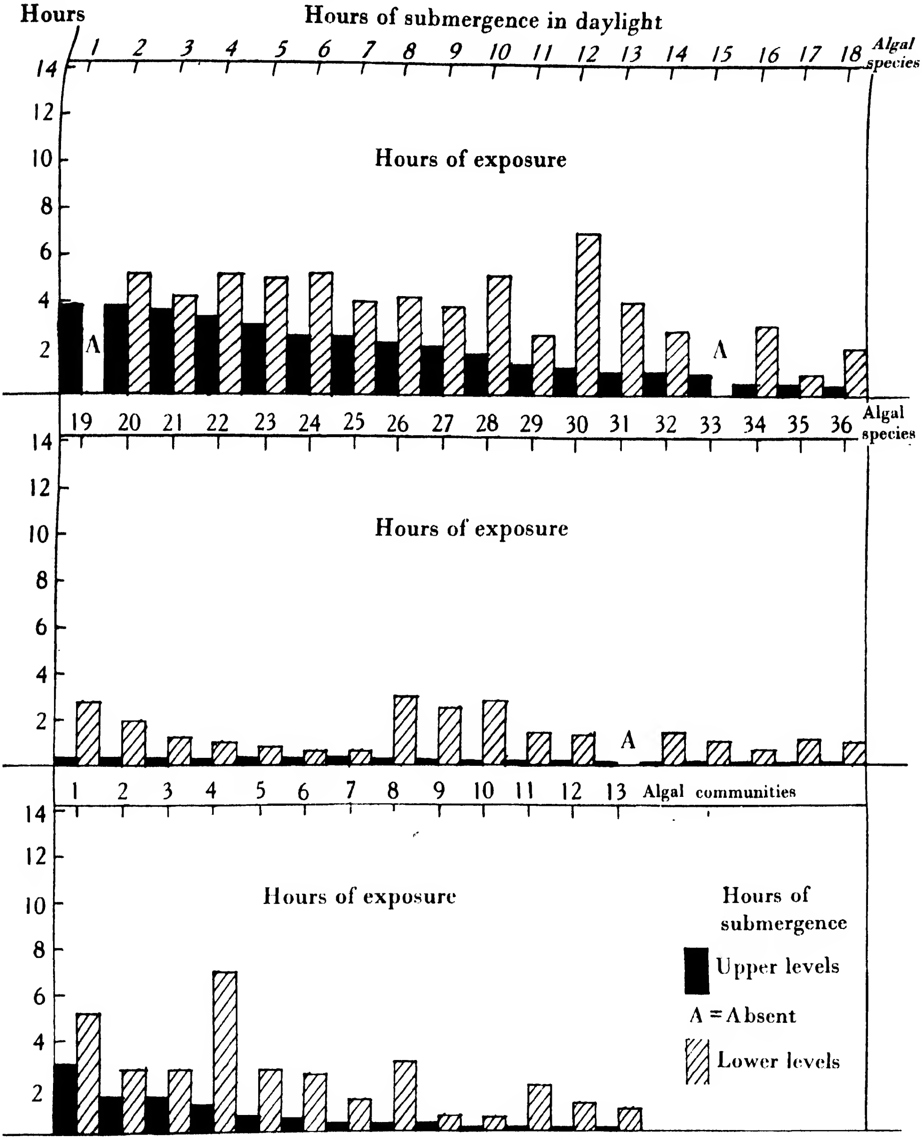


FIG. 5. Algal species and communities and hours of submergence in daylight at the limits of their vertical ranges. Numbers correspond to the order in Figs. 2 and 3, 1 being the lowest species or community.

true salt marsh algae descend below mean sea-level, though one or two have their lower limit near it.

Hours of submergence in daylight

It might have been thought that the inhibition of the passage of light by silt-laden water would be an important factor. The analysis of Table II, however, shows that it is doubtful whether this factor would have any significance above a level of $-1{\cdot}00$ ft. I.Z.L., but it is perhaps worth while noting that only two phanerogamic species have lower limits below $-1{\cdot}0$ ft. (*Zostera nana* and *Salicornia herbacea* agg.). It may well be, therefore, that the lower limit of the phanerogams is partially determined by the degree of submergence in daylight.

Summary

This study of the tidal factor has served to emphasize four general features.

(*a*) The marshes can be divided into two sets, upper and lower, which exist under considerably different conditions of submergence and exposure. For the Norfolk marshes $+1{\cdot}10$ ft. I.Z.L. (8·10 ft. O.D.) is regarded as forming the delimiting level. The plants living on these marshes will be subject to the same difference of conditions, and it is worth noting that of the phanerogams studied, twelve species occur almost exclusively on upper or lower marshes whilst only six are found to frequent both. Twenty-seven Algal species live almost entirely on either the upper or lower marshes and only nine on both. It therefore seems as if the general conditions of the upper and lower marshes have a very real significance for the plants.

(*b*) One of the characteristic features of the upper marshes is the long non-tidal exposure in summer when desiccation may be severe. It was pointed out that the algal species which occur on high marshes are those which are peculiarly suited to withstand desiccation.

(*c*) None of the phanerogams studied have lower limits below mean sea-level.

(*d*) It is perhaps more than a coincidence that only two phanerogams descend below $-1{\cdot}00$ ft. I.Z.L., the level at which the factor of submergence in daylight may begin to operate.

It is probable that the tidal factor has a greater influence upon the phanerogams than upon the algae, especially since the occurrence of the latter may be determined by other factors (phanerogamic vegetation, light, and space relations).

Table IV is a summary of the principal conditions operating on the upper and lower marshes. A highly significant feature of this table is provided by a comparison of the maximum period of non-tidal exposure (10 days) on the lower marshes, with the minimum period (22 days) on the upper marshes. From Table II it can be seen that between $+1{\cdot}09$ ft. and $+1{\cdot}23$ ft. I.Z.L. (1·75 in.) the rise of level is sufficient to bring about this big change in non-tidal

exposure, occurring between May and July at the hottest time of the year. This serves to emphasize more clearly the significance of the upper and lower marshes.

Table IV

Lower marshes	Upper marshes
(*a*) Below +1·10 ft. I.Z.L.	(*a*) Above +1·10 ft. I.Z.L.
(*b*) More than 360 submergences per annum	(*b*) Less than 360 submergences per annum
(*c*) Maximum number of submergences in December–January April, May July October	(*c*) Maximum number of submergences in March–April Sept., October
(*d*) Month with maximum number of submergences Below +·10 ft. generally July or December Above +·10 ft. October	(*d*) Month with the maximum number of submergences Below 3·10 ft. October Above 3·10 ft. September and October
(*e*) Maximum periods of non-tidal exposure spring. More rarely autumn	(*e*) Maximum periods of non-tidal exposure Below 3·0 ft. June–July 3·0 to 3·15 ft. Dec.–January Above 3·15 ft. June–August
(*f*) Minimum period of non-tidal exposure 22 days	(*f*) Maximum period of non-tidal exposure 10 days
(*g*) More than 1·2 hr. submergence per diem in daylight	(*g*) Less than 1·2 hr. submergence per diem in daylight

Table V is a summary of the distribution of the plant species and communities on Scolt Head Island in relation to the upper and lower marshes. The ranges of the species and communities are related to I.Z.L. (+7·0 ft. O.D.).

It cannot be too strongly stressed that these results only apply to the 4½ miles of marshes on Scolt Head Island, but at the same time they probably provide an indication of the relation of the different species towards the tidal movements on the whole coastline between Lynn and Blakeney.

As a basis for future experimental work, it may be suggested that the downward spread of Phanerogams existing on the upper marshes is limited by the increasing number of submergences, whilst the upward spread of phanerogams existing on the lower marshes may be limited by the increasing degree of exposure.

III. The water-table, soil aeration, and drainage

Introduction

In Section II an analysis of tidal phenomena on salt marshes is presented, and it is now proposed to study in more detail the operation of the tides upon the physical characters of the environment. The water-table was selected for primary investigation because the water supply is of fundamental importance to plants. Although much research has been done on the ecology of salt marshes, so far no real quantitative evidence has been collected to determine what changes, if any, take place in the soil water-table of the marshes, and whether such water movements can be correlated with the rise and fall of

Table V

Lower marshes Below +1·10 ft. I.Z.L.		Above and below +1·10 ft. I.Z.L.		Upper marshes Above +1·10 ft. I.Z.L.	
		Communities			
Phanerogams					
Salicornietum	−0·88 to +1·09 ft.	Late Asteretum	+1·04 to 1·93 ft.	General salt marsh	2·37 to 2·87 ft.
Asteretum	−0·5 to +1·28 ft.	Obionetum	0·59 to 2·9 ft.	Sea meadow	2·16 to 2·97 ft.
Creek Asteretum	−0·55 to +0·16 ft.	Suaedeto-Salicornietum	0·4 to 1·6 ft.	Juncetum	2·77 to 3·49 ft.
Zosteretum	−3·25 to −0·18 ft.			Plantaginetum	1·85 to 3·11 ft.
				Sandy Obionetum	2·07 to 2·40 ft.
				Obioneto-Staticetum	1·19 to 3·02 ft.
				Obioneto-Glycerietum	2·24 to 3·11 ft.
Algae					
Muddy Chlorophyceae	−3·2 to −0·9 ft.	Enteromorpha minima	−0·55 to +1·85 ft.	Phormidium autumnale	0·95 to 2·7 ft.
Vernal Ulothrix	−0·55 to +0·6 ft.	Bostrychia-Catenella	−0·4 to +2·55 ft.	Gelatinous Cyanophyceae	2·25 to 2·9 ft.
Low Sandy Chlorophyceae	−4·6 to +1·15 ft.	Fucus limicola	−0·55 to +1·6 ft.	Autumn Cyanophyceae	2·25 to 3·1 ft.
		Sandy Chlorophyceae	−0·9 to +2·85 ft.	Enteromorpha clathrata	1·10 to 3·2 ft.
		Bostrychia-Pelvetia	+0·15 to 3·2 ft.	Rivularia-Phaeococcus	1·45 to 3·25 ft.
		Species			
Phanerogams					
Zostera nana	−3·25 to −0·18 ft.	Aster tripolium	−0·55 to +2·04 ft.	Armeria maritima	2·02 to 2·87 ft.
Salicornia perennis	−0·55 to +0·83 ft.	Salicornia herbacea	−2·91 to +2·79 ft.	Triglochin maritimum	1·04 to 3·11 ft.
Spartina stricta	0·44 to 1·02 ft.	Obione portulacoides	−0·34 to +3·17 ft.	Spergularia media	1·04 to 3·17 ft.
		Suaeda fruticosa	−0·34 to +3·36 ft.	Glyceria maritima	1·19 to 3·36 ft.
		Suaeda maritima var. flexilis	0·42 to 2·79 ft.	Plantago maritima	1·85 to 3·11 ft.
		Limonium vulgare	0·93 to 3·17 ft.	Artemisia maritima	1·36 to 3·49 ft.
				Juncus maritimus	2·77 to 3·49 ft.
				Statice reticulata	2·24 to 3·36 ft.
				Obione portulacoides var. parvifolia	1·54 to 3·36 ft.
Algae					
Cladophora expansa	−1·6 ft.	Enteromorpha minima	−1·9 to +1·4 ft.	Calothrix scopulorum	1·55 to 2·55 ft.
C. flexuosa	−3·2 to −1·55 ft.	Fucus caespitosus	−0·55 to +1·4 ft.	Fucus vesiculosus ecad. muscoides	+1·6 ft.
Vaucheria Thuretii	−2·1 to −1·33 ft.	Enteromorpha torta	−1·4 to +2·4 ft.	Phormidium corium	1·35 to 2·9 ft.
Cladophora fracta	−3·2 to −1·2 ft.	Pelvetia canaliculata forma libera	0·2 to 1·6 ft.	Endoderma perforans	1·5 to 2·9 ft.
Fucus spiralis	−2·9 to −0·9 ft.	Enteromorpha prolifera var. tubulosa	−0·55 to +1·7 ft.	Calothrix pulvinata	2·0 to 2·9 ft.
Enteromorpha compressa	−3·25 to −0·3 ft.	Monostroma spp.	0·4 to 2·8 ft.	Nostoc commune	2·2 to 2·9 ft.
Fucus platycarpus	−1·9 to −0·3 ft.	Rhizoclonium implexum	−0·9 to +3·1 ft.	Phaeococcus adnatus	2·3 to 2·9 ft.
Monostroma Grevillei	−2·2 to −0·2 ft.	Catenella repens	−0·35 to +3·15 ft.	Vaucheria sphaerospora	0·9 to 3·2 ft.
Phyllitis Fascia	−1·55 to +0·1 ft.	Bostrychia scorpioides	−0·55 to +3·2 ft.	Ent. clathrata var. prostrata	0·95 to 3·2 ft.
Fucus vesiculosus var. evesiculosus	−3·2 to +0·4 ft.			Spirulina major	+3·3 ft.
Entermorpha micrococca	−0·55 to +0·9 ft.			Phormidium autumnale	0·95 to 3·3 ft.
E. prolifera	−3·25 to +1·05 ft.			Rhizoclonium arenosum	1·55 to 3·3 ft.
				Lyngbya spp.	2·15 to 3·3 ft.
				Microcoleus chthonoplastes	1·3 to 3·4 ft.
				Rivularia atra	1·6 to 3·4 ft.

the tides. An adequate water supply is essential for the satisfactory performance of the physiological processes of plants, whilst if too much water is present the soil becomes waterlogged, conditions may become anaerobic, and only certain plants can thrive. The water supply of an area is therefore of great importance in an ecological investigation, particularly so in an area of salt marshes, which are frequently subject to tidal influences. Theoretically, the ideal conditions for such an investigation would be a series of marshes arranged in increasing height above mean sea-level, each supplied by a branch from a main creek. This ideal is expressed diagrammatically in Fig. 6, where the highest marsh will be at the level of the highest spring tides, because slow mud

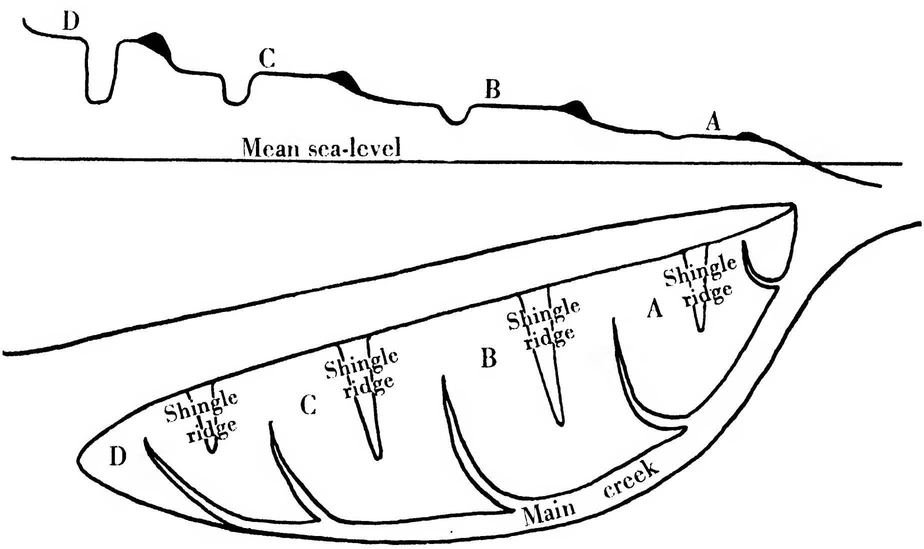


FIG. 6. Ideal series of salt marshes—in plan and section—increasing in height with distance from sea.

deposition still continues at the highest level reached by the tides. A certain amount of "settling" on older marshes may, however, render their differences in height over slightly younger marshes almost negligible. Of these marshes A is the youngest and would be a bare sand or mud flat with some plants of *Salicornia* spp. An examination of these diagrams suggests that the movements of the water-table in the different marshes would not be similar. The lower the marsh the more frequent the tidal inundations and hence the greater would be the waterlogging of the soil. Also, the depth of mud present will be greater on older marshes and this will affect the rate of drainage. The conditions of existence, therefore, on the lower marshes would, in general, be expected to be more adverse to plant life than those on higher marshes.

The behaviour of the tide in relation to salt marshes may be considered under two heads.

(*a*) Access of water to a marsh.
(*b*) Removal of water from a marsh.

Access of water to a marsh

At low tide the sea will be absent from the greater part of the creek systems, because most of these do not descend below mean sea-level, and hence only drainage water and water from springs will be left in the creeks. As the tide rises it enters the creek systems and major and minor creeks are gradually filled. When the tide enters the creeks lateral seepage of water through their walls becomes a possibility. The rate of this seepage, however, will depend upon a number of factors, of which the chief will be the texture of the marsh soil. A marsh built up of mud will offer a high resistance to the subterranean passage of water, whereas a marsh whose soil consists of sand or shingle layers at different depths, will provide, through these layers, a path of easy movement for the water. The Norfolk salt marshes are built upon a sand or shingle foundation, and wherever either of these is exposed in a creek lateral seepage will be facilitated. Usually the younger the marsh the greater the exposure of sand, whilst with increasing age the mud deposit becomes thicker and thicker over the sand. This mud covering along the creek banks must alter to some extent the rate of lateral seepage.

Apart from the geological composition, the time of commencement of lateral seepage into the marsh will be determined by the height of the water-table in the marsh in relation to that of the tide. Seepage will only commence when the height of the tide in the creeks is greater than that of the marsh water-table. Until this state is reached water will continue to drain out into the creeks. The greater the height of the tide above the water-table, the greater should be the rate of lateral seepage. The water entering the soil will replace air in the pores, and the lateral seepage will be facilitated if this air can escape fairly readily, but if it cannot, then the seepage will probably be largely replaced by a pressure transmission. The extent of the subterranean area affected by lateral seepage will depend upon:

(*a*) *Distance apart of the creeks.* The water movement being greatest in areas close to the creeks.

(*b*) *Size of the creek.* The larger and deeper the creek the greater will be the area exposed through which lateral seepage may occur. The importance of this factor is ultimately determined by the texture of the marsh soil.

(*c*) *Height of the marsh above mean sea-level.* The higher the marsh the longer will it take for the creeks to be filled, and seepage will also be slow because of the mud covering to the creek banks. On low marshes the seepage will be relatively greater because much sand will still be exposed. Although the tide will flood a low marsh long before it floods a high marsh, some lateral seepage

will still continue in the former even after it is flooded. This is rendered possible because the stiffness of the surface mud makes downward drainage from the flooding tide very slow, and hence the principal water movement will still be lateral. In contrast to the above, marshes built of soft mud will become saturated almost immediately when flooded, both from above and laterally.

Finally, depending upon the size of the tide and the height of the marsh, the creeks become full and the marsh is flooded. The lowest marsh (marsh A in Fig. 6) will be flooded first, and as the water covers the marsh the rate of rise will become slower as a larger area is available over which the water can spread. Marsh B will be the next to be flooded and so on. Field observations show that the time of high tide on a marsh depends upon the position of the marsh in relation to the foreshore. If there is a big spring tide the ebb will have occurred on the foreshore a considerable time before it begins on marsh D. A shorter interval elapses between the turn of the tide on the foreshore and on marsh B. There is therefore a well-marked lag between points at different distances from the open sea. This lag in time may be as much as 45 min. with a big spring tide, whilst with a neap tide it may be negligible. The presence of a lag indicates also that a gradient of water must exist from the higher marshes to the mouth of the main creek, but no figures are available to illustrate the magnitude of this gradient.

As salt marshes are generally of a relatively uniform height the time of flooding of a marsh is more or less sharply defined, a feature that should be contrasted with the ill-defined time of emergence of the marsh surface during the ebb.

Removal of water from a marsh

With neap tides the phases of removal of water from a marsh are similar to the later stages seen in the ebb of a big spring tide, and hence need not be recapitulated. During a flooding tide the first phase in the ebb is the removal of the bulk of the surface water by superficial drainage into the creek systems. In this process miniature waterfalls are abundant along the edges of the creeks where they tend to cut away the sides, and these waterfalls are probably the principal agents in widening the creeks on the Norfolk marshes. Because of slight depressions in the ground some water is left in pools, and for this reason the time of exposure of the marsh is not so clear cut as that of submergence. The water left in the pools disappears through evaporation and downward drainage. The rate of its disappearance will be determined by the season of the year (which controls rate of evaporation), the humidity of the air, and the number of flooding tides that have preceded the one under consideration. The greater the number of preceding tides the longer will the pools persist, because the ground is approaching more and more towards saturation. The downward drainage of this water, however, will result in a gradual rise of the soil water-table during the spring tide periods.

Until the height of the ebbing tides in the creeks has fallen below that of the soil water-table, lateral seepage into the marsh through the creek walls

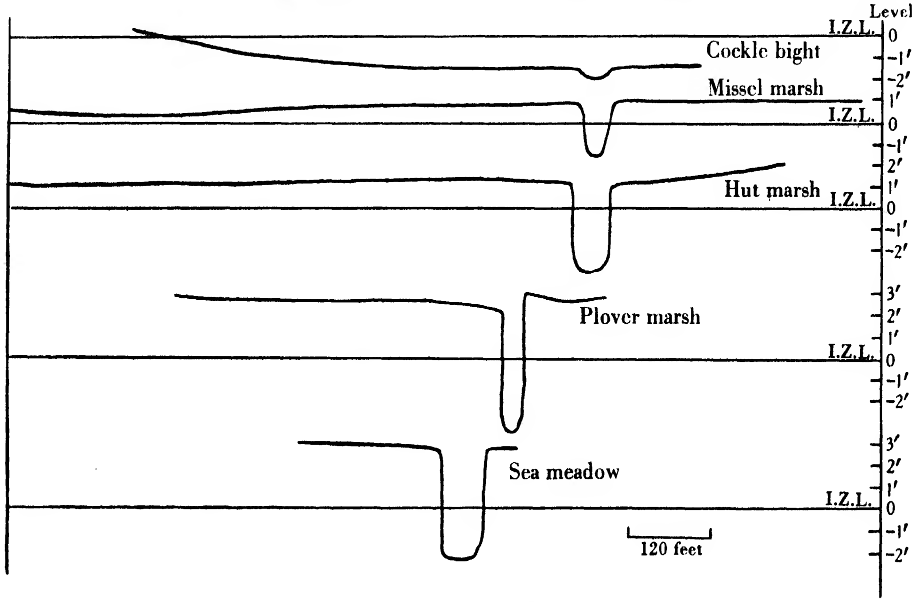


FIG. 7. Levels of salt marshes on Scolt Head Island in relation to island zero level.

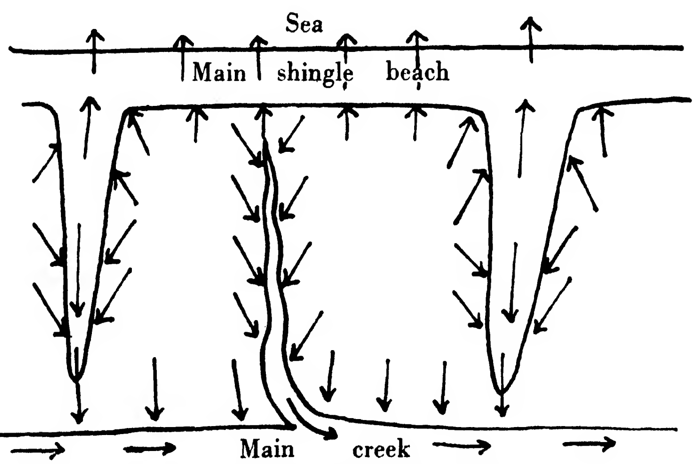


FIG. 8. Lines of lateral drainage off a marsh.

will continue. Once the tide has fallen below the height of the soil water-table then outward drainage from the marsh into the creek will begin and continue until the next tide. The rate of this outward drainage will depend upon the same factors that influence lateral seepage into the marsh.

The general drainage of soil water will be expected to follow the lines of least resistance, and the presence of shingle, or shingly sand, provides such outlets. Since the marshes are above sea-level it may be expected that several lines of subterranean drainage will be open, in contrast to the superficial drainage which is conducted directly into the nearest creeks. Areas near creeks will drain gradually into them, but of the other areas, those nearer the main creek will drain into it via the lateral shingle ridges, whilst areas nearer the foreshore will drain directly into the sea via the lateral ridges and the shingle underlying the dunes.

The salt marshes of Scolt Head Island, although not arranged in an ideal sequence, conform closely to the theoretical set postulated above (cf. Fig. 7). At Scolt, it is possible at low tide to see drainage taking place all along the foreshore at the base of the shingle ridge bearing the main line of dunes. The lines of lateral drainage over a Norfolk marsh may therefore be expressed as in Fig. 8.

The soil

The movements of the water-table depend upon the composition of the marsh soil and also upon the physical properties of its different strata. A detailed geological study has been made of the salt marshes of Scolt Head Island (Steers, 1934), and this has shown that the marshes are very variable in composition. There is a varying depth of silty surface mud which may lie on top of sand or on a clay-mud deposit. Occasional deep pockets of a very stiff clay are encountered, and it was also observed that the surface mud stratum thickened near the creeks. This is to be expected because mud deposition takes place here more rapidly; it must therefore have a major influence upon the rate of lateral seepage. The shingle ridges extend much further under the marshes than would be supposed from surface indications, and this opens up lines of drainage over a far greater area than might at first be expected. The rate of movement of the water-table will vary greatly, therefore, depending on whether the strata is composed of sand, shingle, or mud.

Although the pore space of a clay soil may be 50 % that of the total volume whereas that of sand may be only 30 %, the flow of water will be more rapid in the latter. This is because of the great resistance offered to water movement by clay soil capillaries in contrast to the relatively larger channels of the sand strata. It is evident, therefore, that resistance to flow is a more potent factor than pore space. A study of the resistance offered by the various strata was made by taking samples of soil at different depths on one marsh, and pressing a straight tube (diameter 1½ in.) into each sample until it contained a continuous layer of soil, 2 in. in height. A measured head of water (1 in.) was put on top of the sample and the time required for the first drop to appear was taken as measuring the rate of air displacement (A.D.). When the rate of dropping was constant the number of drops falling per unit time was also noted and its

reciprocal taken as a measure of soil resistance (R.). The method is somewhat primitive and not free from errors but it nevertheless indicated that the clay mud had the greatest resistance whilst the surface mud often had nearly as much. The actual results are set out in Table VI. Any water-table movements in salt marshes must be considered in close relation to the structure of the soil and its physical properties.

Technique

The investigation was commenced by using pits dug into the marshes at strategic points. These were soon abandoned because they filled up at flooding tides, and subsequent drainage was so slow that they did not give any true indication of the absolute height of the water-table. During neap tides, however, their results confirmed those obtained by other methods. In order to escape the difficulties created by flooding, tubes were sunk into the marsh with their lower portions perforated to allow the access of water. Measurements of the water movements were made by means of graduated cane sticks. These tubes gave more exact results, but as time went on it was realized that two errors were involved.

(*a*) The water movements depended on whether the perforated portion was situated wholly in a sand or clay stratum or penetrated both. The holes, also, were apt to become choked with clay mud.

(*b*) Evidence accumulated which suggested that the upward movements of the water in the soil took place against a pressure exerted by the air enclosed in the surface clay. The tubes, by opening up an outlet to the surface, reduced this pressure and water movements took place more rapidly and to a greater extent than in the untouched soil.

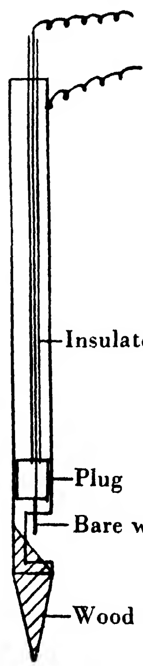


FIG. 9. Electrical recorder. A plug on a strong steel wire closed the lower hole when inserting recorder into soil. This was then replaced by the centre electrode.

The tubes were finally used in conjunction with electrical recorders of the type illustrated in Fig. 9. These were used singly or in a series plunged to different depths. It can be appreciated that their structure and *modus operandi* obviated the two errors inherent in the tubes. During the process of inserting the recorders into the soil a plug was lowered to the base of the tube so that soil could not block the lower opening. When a tube had been forced down to the required depth the plug was withdrawn and the centre electrode put in place. A voltmeter and 6 V battery completed the circuit, the voltmeter recording the precise moment when the water made contact with the bare wire at the base of the tube.

Table VI. *Rate of air displacement* (A.D.) *and soil resistance* (R.) *to passage of water through salt marsh soils*

Pits	1		2		3		4	
Soil	A.D.	R.	A.D.	R.	A.D.	R.	A.D.	R.
Silty clay	2 sec.	0·008	25 min.	0·006	2 min. 40 sec.	1·000	45 sec.	0·250
Sand 9 in. to 1 ft.	—	—	2 sec.	0·002	2 sec.	0·053	$7\frac{1}{2}$ sec.	0·004
Clay 1 ft. 6 in. to 2 ft. 3 in.	$3\frac{1}{2}$ hr.	0·016	72 hr. +	0·071	50 sec.	0·010	13 hr. +	1·00 for 105 min.

Pits	5		6			7			9	
Soil	A.D.	R.	A.D.	R.		A.D.	R.		A.D.	R.
Silty clay	20 sec.	1·00 for $17\frac{1}{2}$ min.	2 min.	0·250	Silty clay	15 sec.	0·125	Silty clay	2 sec.	1·0 for 16 min.
Sand 9 in. to 1 ft.	2 sec.	0·004	5 sec.	0·003	Silty clay	22 sec.	0·250	Sand	2 sec.	0·004
Clay 1 ft. 6 in. to 2 ft. 3 in.	36 hr. +	1·00 for 35 min.	—	0·333 for 4 min.	—	$15\frac{3}{4}$ hr.	0·333 for 4 min.	Clay	14 min.	0·083

Resistance (R.) is given as the reciprocal of drops per 2 min. unless otherwise stated.
Rate of air displacement (A.D.) is indicated by the time required.

The pits, tubes, and recorders were distributed on the marshes at measured intervals, usually at right angles to a creek so that the lateral seepage could be readily measured.

Non-flooding tides

In order that the tides may produce any effect on the level of the water-table of a marsh they must rise to a certain height, and the more they rise

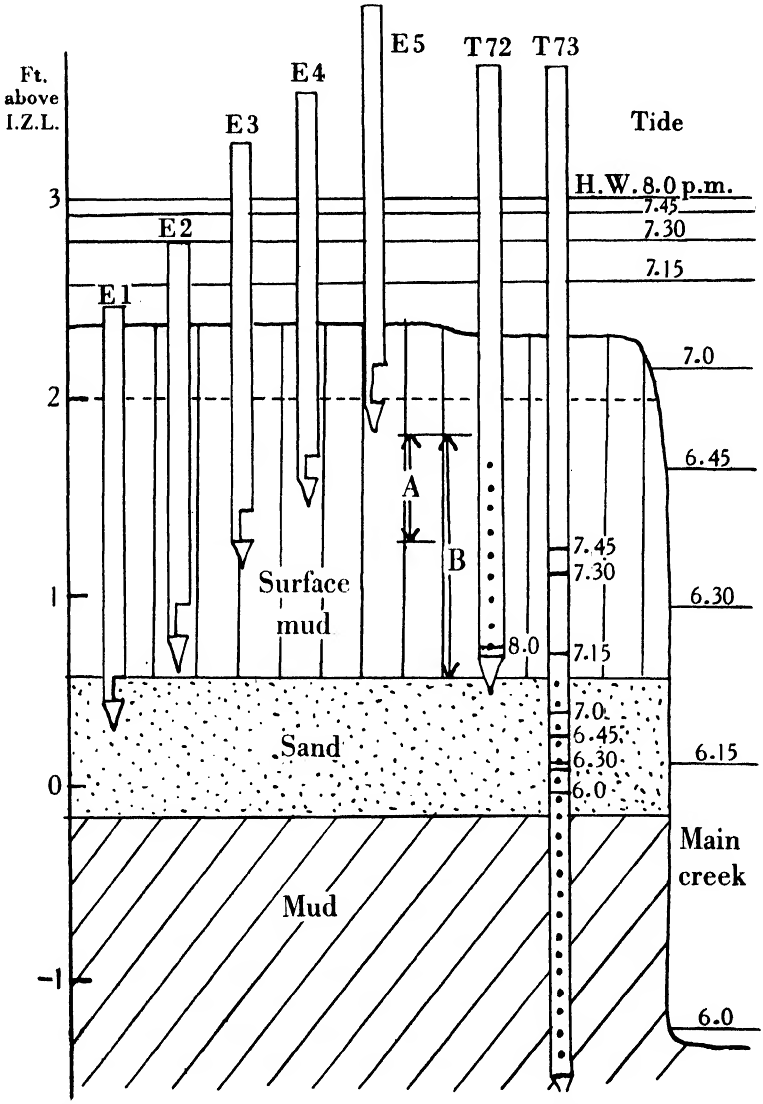


FIG. 10. Plover marsh, near main creek. Evening tide, 27 June 1934. E 5 recorded at 7.30. E 1 and E 2 flooded before recording. A = definite aerated layer, B = probable extent of aerated layer.

above this initial level the greater will be the effect upon the water-table. The absolute height of this initial level for any given place on a marsh will depend upon four factors.

(i) *The distance from the creek.* The nearer the area is to a creek the greater will be the effect on the water-table, and the sooner will the influence of the tide be felt, assuming that the soil structure is homogeneous throughout.

(ii) *The size of the nearest creek.* It is reasonable to suppose that the larger the creek and the more water it contains the greater will be any effect upon the water-table, so long as lateral drainage into the marsh is correlated with inflow along the creek.

(iii) *The height of the marsh.* The lower the marsh the more often will the water rise to heights that will influence the water-table.

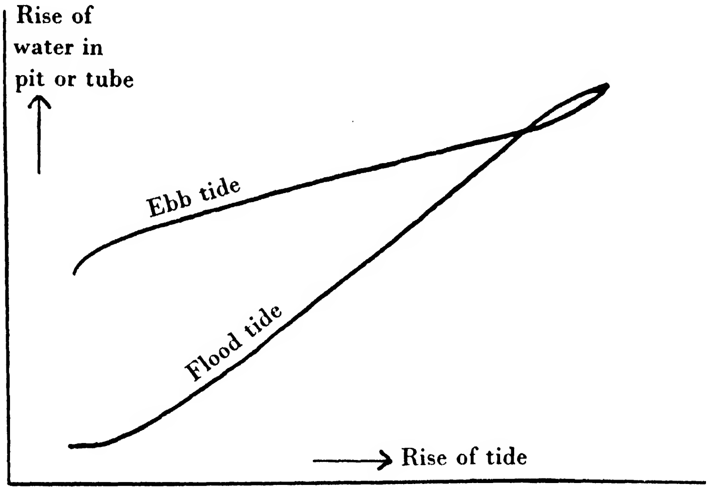


FIG. 11. Relation of water-table movements to tidal rise and fall.

(iv) *Strength and direction of the wind.* The effect of wind is to render the water-table of an area liable to tidal influence on days when it would not normally be affected, and vice versa.

The use of pits and tubes indicated that the water rose slightly during the period round about high tide, the extent of the rise being a function of distance from creek and maximum height of the tide. The use of the electrical recorders confirmed these earlier experiments. On 26 June 1934, although the tide rose to +2·04 ft. I.Z.L., recorders E1 to E5 (Fig. 10) were not affected. On the next morning, when the tide rose to +2·21 ft. I.Z.L., only E1 gave a record. It may be stated, therefore, that during non-flooding tides there may be a rise in the soil water-table during the time the rising tide is in the creek, the rate and magnitude being dependent upon the factors described previously, and also that there will be a lag in the rise of the soil water-table due to the soil resistance.

The results from both the pits and tubes were analysed in order to determine their relationship with the tidal movements. Allowance was made for the observed time lag of individual tubes, and then the rise and fall of the water in each tube or pit was plotted against the rise and fall of the tide as indicated by pit 48 (a stake in the main creek). The resulting curves were composed of two portions, one corresponding to the flood tide and one to the ebb. All the

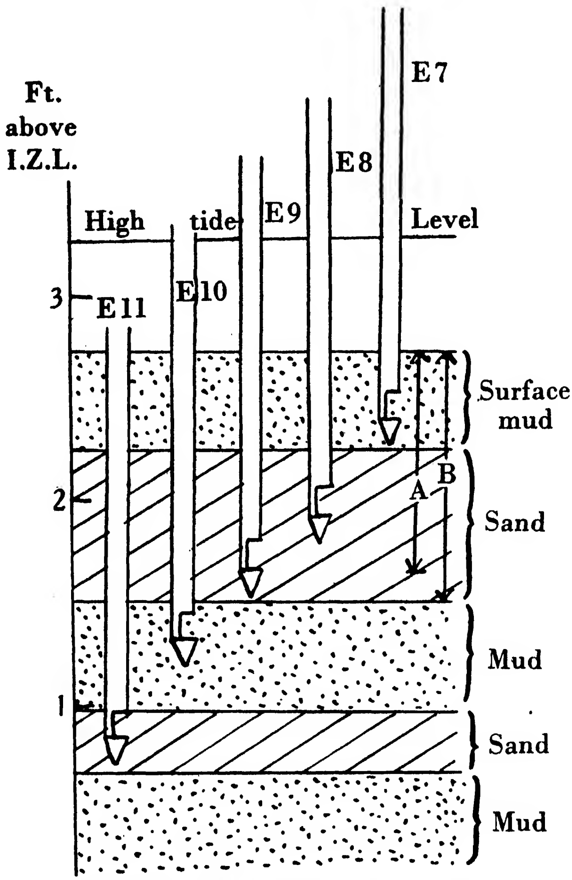


FIG. 12. Plover marsh, away from a creek. Morning tide, 28 June 1934. E 10, E 11 flooded; E 11 recorded, E 7 to E 9 no record. A = definite aerated layer, B = probable extent of aerated layer.

curves conformed to a general type similar to that shown in Fig. 11. The conclusion is that the relationship is not absolutely linear, but in practice the error will not be great if the relationship is regarded as linear.

Flooding tides

The use of the electrical recorders revealed the fact that at flooding tides, even when the tide was actually covering the marsh, the soil water-table rarely rose into the surface mud layer. In other words, there was always an *aerated*

soil layer between the water-table and flooding tide. This was true of all the marshes (except bare sand or mud flats) irrespective of height or position.

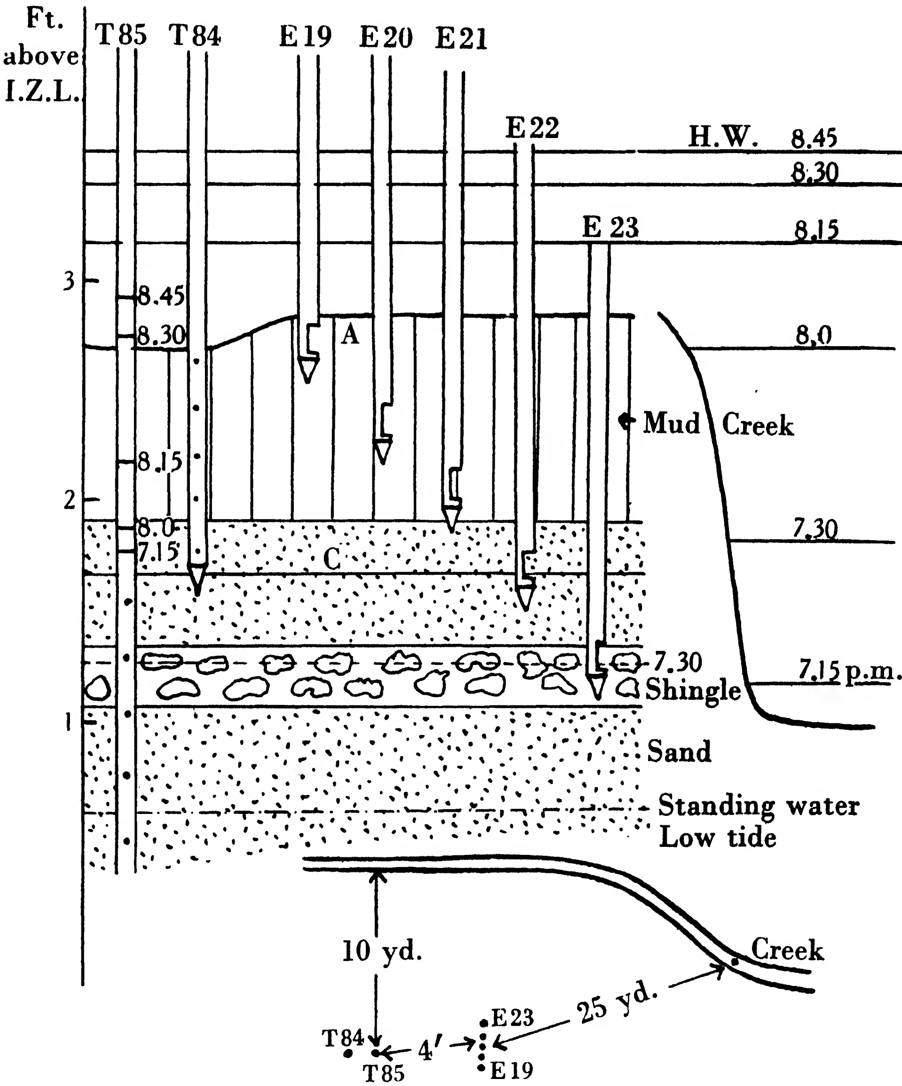


FIG. 13. *Juncetum* near Brancaster Staithe, 27 July 1934, evening tide. E 22 flooded, E 23 recorded, E 19 to E 21 no record, T 84 remained dry. A–C marks the definite aerated layer.

In Fig. 10 is depicted the conditions existing at high water near a creek on one of the Scolt Head marshes. E 5 recorded, whilst E 4 and E 3 did not record at any period. The area bracketed A was therefore free from a continuous water-table, and this area probably extended downwards to that marked B. Fig. 12

illustrates a similar condition for the same marsh but at some distance from the creek. Area A again represents the observed aerated layer whilst B marks its probable extent, because E10 was flooded from above before it recorded. Fig. 10 also demonstrates the relative difference of movement that can take place in a tube which has its perforations in sand (T73) as compared with one in clay-mud only (T72). Similar results were obtained from a number of other marshes. Fig. 13 shows some that were obtained from a mainland marsh near Brancaster Staithe. A–C represents the observed boundary of the aerated layer because T84 remained dry throughout.

The aerated layer

Further proof of the existence of an aerated layer has been obtained from other sources. Its existence, previously unknown, may be of the utmost importance in understanding how plants can live on salt marshes, especially species not normally regarded as halophytes (e.g. *Phragmites*).

(1) If, during a flooding tide, a stick is pushed for a few inches into the surface mud and then withdrawn, bubbles of air appear. This result is obtained equally well after a number of flooding tides, so that the aerated layer persists throughout a spring tidal cycle. After a period of dry weather when the soil becomes cracked, bubbles of air also appear from the cracks as soon as the tide covers the marsh.

(2) The same experiment carried out on the Merse lands of the Nith estuary (Morss, 1927) provided similar results, which at the time were regarded as indicating the presence of a lower aerated layer.

(3) The use of manometers on a number of marshes not only indicated the presence of an aerated layer, but also demonstrated the fact that at a flooding tide the air in this layer undergoes compression. Fig. 14 illustrates results from three manometers[1] which were put down a few inches from a large creek. The diagram records the readings obtained on 27 June 1934, during the evening tide. Only a final reading was obtained from M2 because it recorded very rapidly during a short absence to read other instruments. It will be noted that the manometers recorded in the sequence that would be expected, the lowest starting first. At high water no record was obtained from E6 so the soil water must have been below the lowest of the gauze cylinders. Fig. 15 sets out the results obtained on two successive days from three manometers put down in a *Juncetum* on a mainland marsh. On 26 July, M1, the lowest, recorded the steepest rise and ultimately overflowed, whilst M2 and M3 followed very similar curves. All three manometers show the tidal influence again on 27 July but the intervening tide had brought about a separation of the initial values.

(4) If two tubes are sunk so that the perforations of one are in the surface mud layer and those of the other in the sand layer, then at a flooding tide a large

[1] Sea-water was the liquid employed in the U-tube.

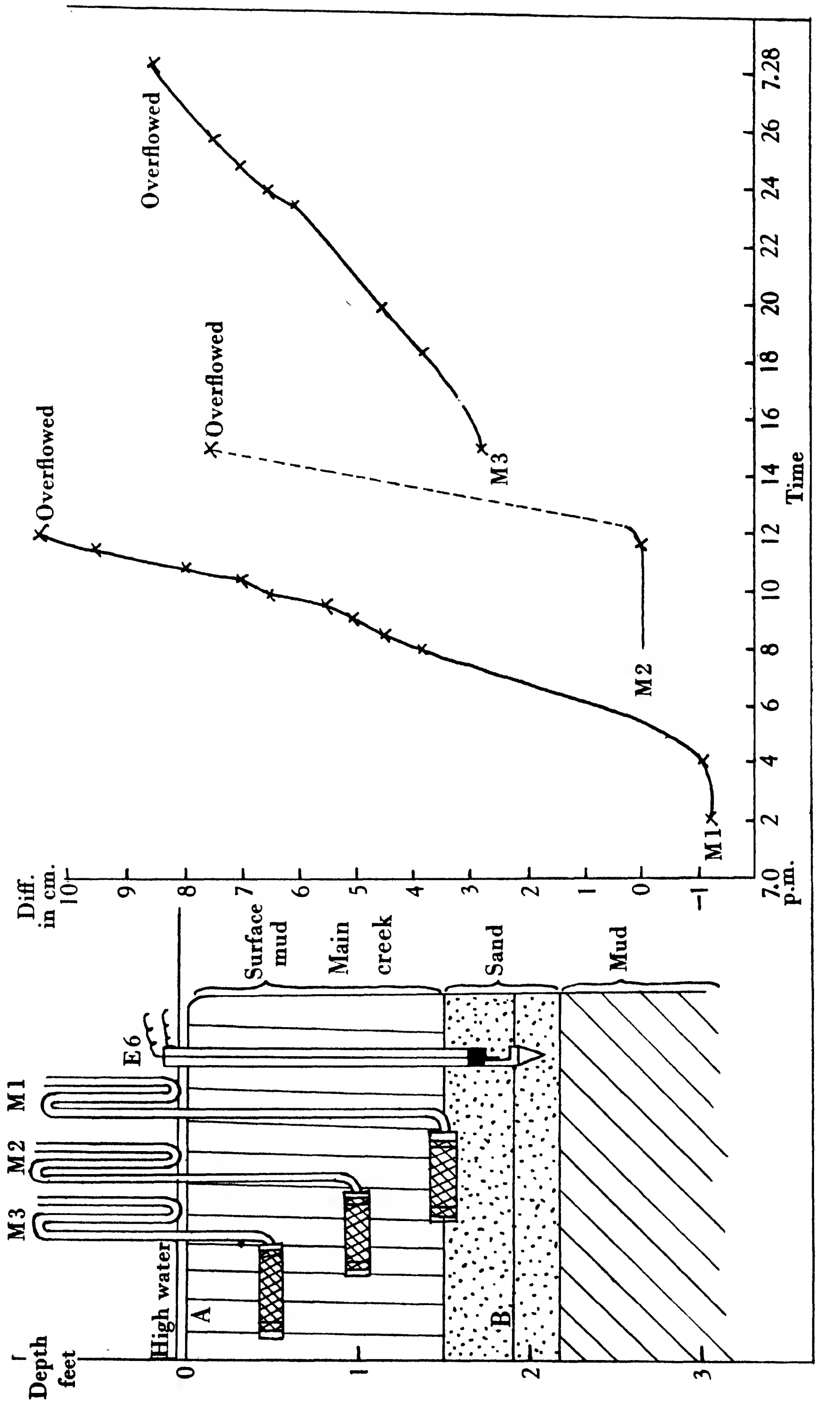


FIG. 14. Manometers, Plover marsh, near creek. Evening tide, 27 June 1934. No record from E6. A–B marks extent of aerated layer.

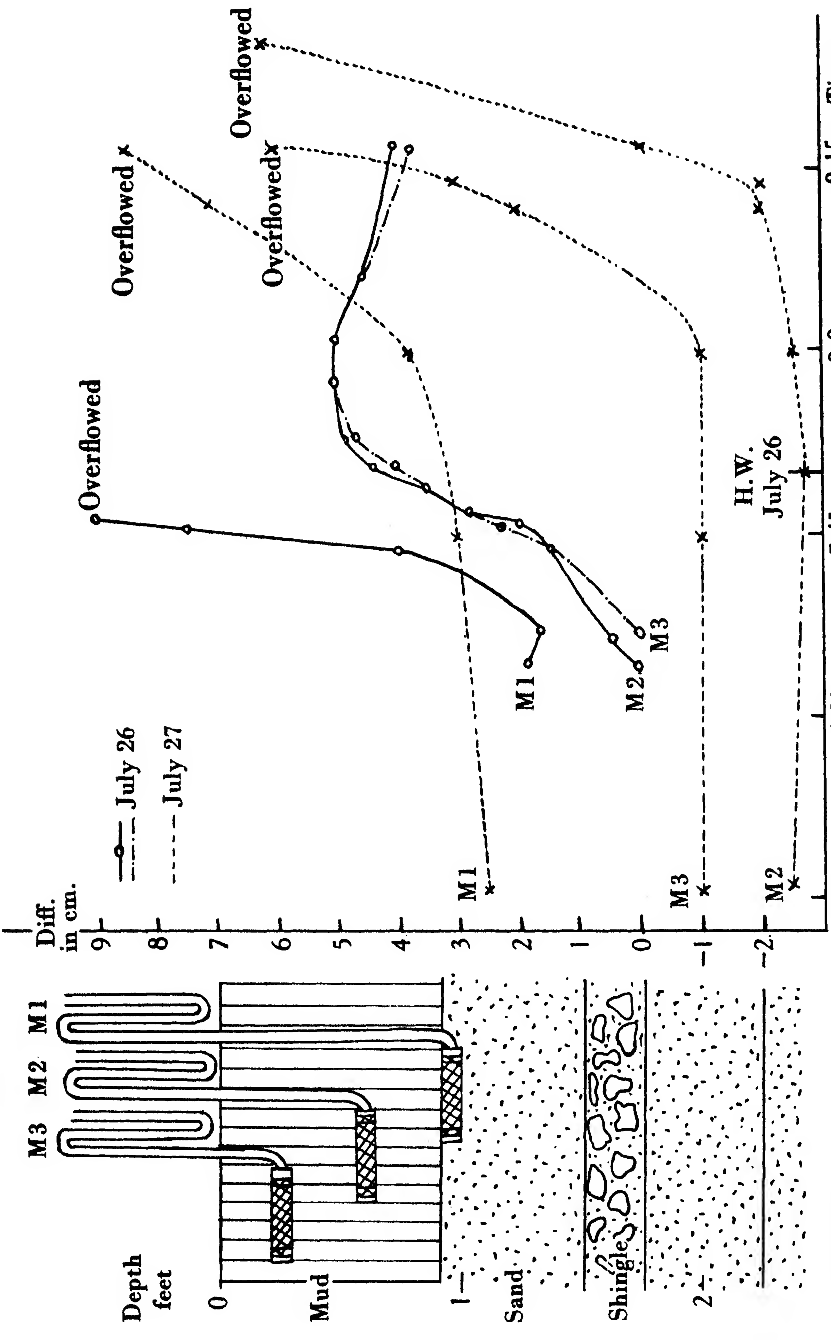


FIG. 15. *Juncetum*. Manometers during evening tides, 26 and 27 July 1934.

range of movement is recorded in the second tube and little or none in the first (cf. Fig. 10).

(5) Some of the expelled air was collected directly into sample tubes containing equal volumes of glycerine and saturated salt solution. With experience the technique does not permit the air to remain long in contact with sea water and hence any CO_2 absorption will be reduced to a minimum. These samples were analysed by Miss Conway at Cambridge. One set (samples A–C) was obtained by collecting samples at 4 yd. intervals in a line at right angles to a creek. The full results are shown in Table VII. These figures demonstrate the fact that the gas enclosed in the surface layers of the marsh soil has a fluctuating composition, not only from marsh to marsh, but also in a single marsh. The high CO_2 content of some marshes may be of significance, but at the same time there are also marshes with a very low oxygen content. Similar results have also been obtained from gas expelled from the soil of New England marshes.

Table VII

	Missel marsh			Missel marsh	N. Missel marsh	Hut marsh	Salicornietum on shingle
	A	B	C				
CO_2	2·99	2·55	3·26	4·22	1·46	0·93	0·88
O_2	1·61	0·82	0·71	1·42	10·5	17·5	18·30
N_2	95·4	96·63	96·03	94·36	88·04	81·57	80·82

(6) An experiment was set up to reproduce the conditions on a marsh at a flooding tide. It was of the type shown in Fig. 16. With a big head of water (8 in.) in the funnel there was very little water movement in the sand, and the only air expelled came through a cut-off *Limonium* root. The water level in the funnel changed but very slowly, and this was partly due to evaporation. It was evident, however, that most of the air was contained in the loculi formed by the decay of old roots, and such loculi could be seen through the glass tube. The presence of these loculi with occluded gas probably explains the low oxygen values cited above, and also why such large bubbles can be obtained by poking a stick into a clay soil.

(7) Prof. T. G. Hill informs me that he also has seen the bubbles issuing from the marsh surface during a flooding tide, giving an appearance to the water of a "magnum of Champagne".

Root systems

When the existence of the aerated layer had been fully demonstrated, the immediate concern was to ascertain whether the distribution of the root systems were correlated with the layer. Since it was impossible to extract the root systems intact because of the stiff clay soil, cubical samples of soil measuring 4 in. on a side were taken at successive depths, crushed up in water, the roots filtered off, dried, and weighed. The root distribution in eight marshes was

investigated in this manner and two typical results are shown in Fig. 17. It is clear that the bulk of the roots are associated with the surface mud layer. Two theories present themselves for consideration:

(*a*) The distribution of the roots is directly associated with the aerated layer.

(*b*) The roots of the plants occur naturally near the surface and so the correlation has no significance. However, the root distribution on the various marshes follows the surface mud strata so closely that it seems to be more than a coincidence.

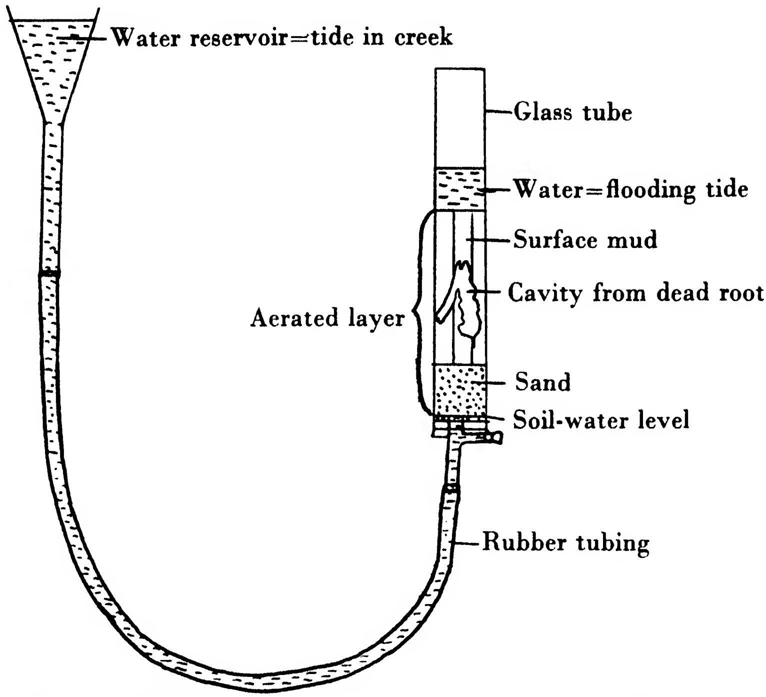
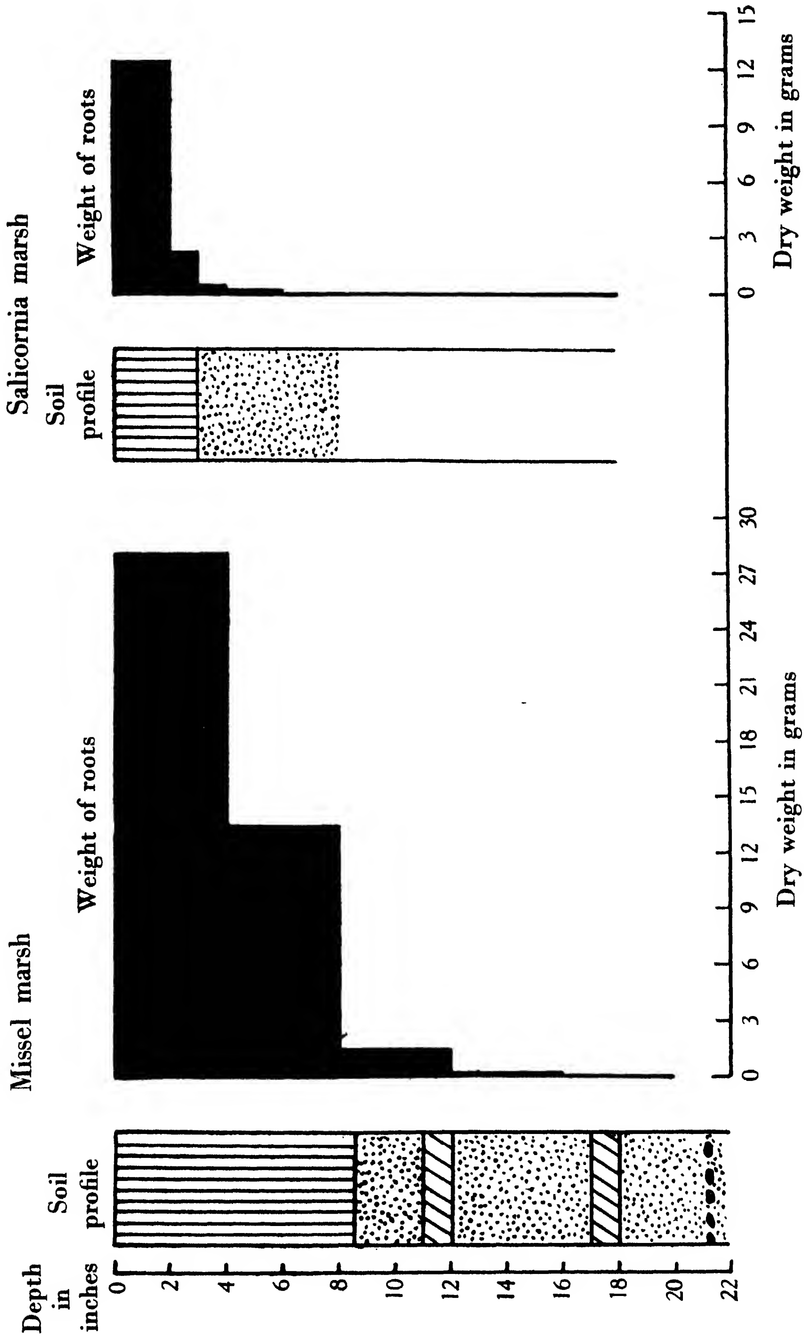


FIG. 16. Artificial demonstration of marsh conditions during a flooding tide.

If (*a*) is the correct interpretation it will then be necessary to determine whether the plants have brought about the presence of the aerated layer through their decaying roots, or whether the mere accumulation of the stiff mud is sufficient. It is probable that the latter is correct to some extent because there are bare areas from which gas can be liberated, not only on the open marsh but also in salt pans.

Spring tidal cycles

Long-period observations were made on a number of marshes in order to determine the changes of water level throughout several tidal cycles. In practice the "spring-neap" cyclic fluctuations have the diurnal fluctuations



Relation of root distribution to soil profile

FIG. 17.

(which have already been described) superimposed upon them. From the mass of evidence available (too bulky to quote in full), it is clear that there is a normal downward gradient of water towards each creek, but this gradient may be obscured temporarily during a spring tide. The water-table usually shows rather a sharp rise towards the period of maximum spring tides and then falls off gradually until the next series. The spring tidal cycles in Norfolk are of two kinds; lesser spring cycles occurring once a month, during which the highest tides do not attain 27 ft. Hull datum, and major spring cycles alternating with the lesser cycles and also occurring once a month. The general water-table of the higher marshes is usually unaffected to any extent by the lesser cycles except for diurnal movements near creeks. Depending upon the height of the marsh, there is a certain critical height which the tides must reach before they exert a permanent influence on the water-table, as apart from the purely temporary diurnal changes.

There is usually a distinct permanent gradient into the shingle laterals bordering each marsh (Chapman, 1937). This confirms the theoretical expectations set out at the beginning of this section. The effect of rainfall on the movements of the marsh water-table appear to be negligible along this stretch of coast. Godwin & Bharucha (1933) showed that on Wicken Fen during the summer months plant transpiration largely controlled the level of the water-table. There is no evidence of such control on any of these Norfolk marshes as yet, and it seems as if any transpiration effects must be masked by the tidal phenomena.

Conclusions

The water-tables of the Norfolk salt marshes are subject to two distinct influences:

(*a*) Diurnal movements induced by the daily tides.

(*b*) Cyclic movements induced by the spring tidal cycles.

(*a*) is only observed within short distances of creeks because of the soil resistance, whereas (*b*) can be traced over the whole marsh. The various features associated with the movements can be summarized as follows:

(1) During the flooding and non-flooding tides there is a marked rise and fall of the water-table in the sand stratum below the surface mud. The range of this movement is greatest near creeks and diminishes with increasing distance from them.

(2) An aerated layer is present in the surface mud and sometimes in the upper sand level also: this layer does not disappear during the spring tidal cycles, but the enclosed air may undergo compression. The heights of the previous tides, together with the depth of mud, are important factors in determining the extent of this aerated layer.

(3) The bulk of the enclosed air is probably contained in cavities left by decaying roots in the lower strata of the surface mud. The occluded gas does

not have the same composition as atmospheric air, and it is probable that entrance and admixture of atmospheric air into the soil is difficult because of the physical nature of the mud.

(4) The principal factors determining the daily movements of the water-table are as follows:

(*a*) *The height of the previous tide.* This has already been shown to determine the initial height of the water-table, and is especially important at flooding tides.

(*b*) *Resistance of the strata.* The movements of the water will be greater in some strata than in others, depending on the relative resistances.

(*c*) *Strength and direction of the wind.* This acts indirectly in so far as it affects the height, not only of preceding tides, but also of the tide under consideration.

(*d*) *The height of the tide* under observation.

(*e*) *The height of the marsh* upon which experiments are being conducted.

(*f*) *Distance from the creek* and *size of the creek.* The nearer the creek the greater will the movements tend to be, and the larger the creek the greater will be the area influenced.

(*g*) *The difference in height at any moment between the tide and the water-table.*

(5) The movement of water in the soil will take place along the following lines:

(*a*) *Lateral seepage.* The rate of lateral seepage will depend on soil resistance and also upon the distance from the creek. So long as the tide in the creek has access to a sand stratum there will be considerable lateral seepage into the marsh. Such seepage will occur during both the flood and ebb tides but in opposite directions.

(*b*) *Downward drainage.* This takes place everywhere and at all times, even during flooding tides, though at such periods it may be masked by lateral seepage. The rate of downward drainage into the various strata is determined largely by soil resistance.

(*c*) *Surface evaporation.* This factor only comes into operation during and after a flooding tide. The extent to which it may influence the volume of water that might drain into the soil is dependent upon the time of year and the type of day. On a fine day in midsummer it might play a very great part in the removal of residual water from a marsh.

(*d*) *Transpiration.* This factor appears to be masked by the tidal phenomena, even in the summer months.

(*e*) *Surface flooding.* This is a means whereby many tons of water are carried over a marsh in a very short space of time. The frequency with which this phenomenon occurs will be dependent upon:

- (α) Height of the marsh.
- (β) Height of the tides.
- (γ) Strength and direction of the wind in so far as it affects the height of the tide.

(6) Finally, the water movements during a diurnal tidal cycle in the soil near a creek, may be represented diagrammatically as in Fig. 18.

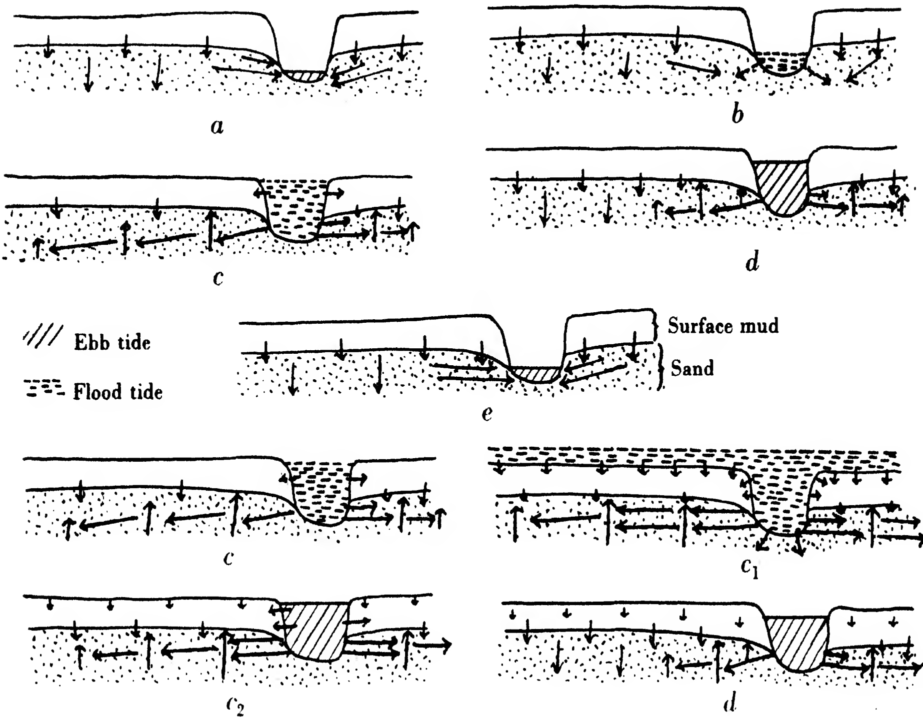


FIG. 18. Water-movements during a diurnal tidal cycle. *a* to *e*, non-flooding tide, c—c_1—c_2—d. flooding tide. Surface mud remains as an aerated layer.

Note. It must be remembered that these results have been obtained from the series of marshes between Brancaster and Burnham Overy on the north coast of Norfolk, but it is probable that they are valid for all the marshes between Lynn and Blakeney, and possibly also for those on the Essex coast.

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THE SOIL COMPLEX IN RELATION TO PLANT COMMUNITIES[1]

I. OXIDATION-REDUCTION POTENTIALS IN SOILS

By W. H. PEARSALL

It has long been recognized that all fertile soils contain bacterial and fungal systems which are capable of breaking down the soil organic matter, and it is known the transformations so produced commonly involve oxidations, though less frequently reductions may also occur. These changes have been largely ignored by field ecologists, and it is the object of the present communication to point out that a comparatively simple technique is now available which may serve to throw some light at least on these activities. The technique involved is that of measurements of the electrical potential of the soil, which, it seems probable, may be interpreted as representing the oxidation-reduction potential.

Theory

Although it is necessary for an understanding of the problems involved to outline the principle underlying these measurements, no attempt will be made to do this in any detail since the admirable summaries of Clarke (1928), Michaelis (1934) and the Needhams (1927) adequately survey different aspects of the general theory and its applications.

While, in the original sense, the terms oxidation and reduction meant chemical changes involving gains or losses of oxygen from the substance changed, widening of chemical theory has of necessity led to the inclusion of other types of reaction in which oxygen may take no part. Thus leucomethylene blue in the presence of oxygen is said to be oxidized to methylene blue although the latter contains no oxygen and differs from the former only in containing less hydrogen, which has been combined with oxygen to form water. In a similar manner cuprous chloride can be oxidized to cupric chloride in acid solution and in the presence of oxygen. Here again though oxygen disappears it is not found in the cupric chloride, the final expression of the change being:

$$4CuCl + O_2 + 4HCl \rightarrow 4CuCl_2 + 2H_2O.$$

But the change from cuprous to cupric salt may take place without involving either hydrogen or oxygen. Thus cuprous chloride may be oxidized to cupric chloride in the presence of ferric chloride—the latter being reduced to ferrous

[1] The substance of three papers under this general heading was delivered as the Presidential Address to the British Ecological Society at its meeting on 9th January, 1937.

chloride. Thus three types of chemical change at least have now come to be included in the extended definition of the term oxidation. Their common and fundamental feature lies in the energy changes involved.

In the study of these phenomena, the relation between ferrous and ferric salts has played historically an important part. As this system is useful in considering certain soil phenomena, the example may be utilized here. The oxidation of ferrous to ferric iron involves simply the loss of an electron:

$$Fe^{++} \rightleftarrows Fe^{+++} + 1 \text{ electron.}$$

As a result of this, differences of electrical potential will exist between solutions containing ferrous and ferric ions. The magnitude of these potentials will vary with the proportions of ferrous and ferric ions present according to the equation:

$$E_h = E_0 - \frac{RT}{F} \log_n \frac{(Fe^{++})}{(Fe^{+++})},$$

an equation which is a particular case of the general form applying to all reversible oxidation-reduction systems.

Calling the reduced substance the reductant and the oxidized form the oxidant, the general form of the equation becomes, using natural logarithms,

$$E_h = E_0 - \frac{RT}{NF} \log_n \frac{(\text{reductant})}{(\text{oxidant})},$$

and converting to Briggsian logarithms at 20° C.,

$$E_h = E_0 - 0{\cdot}058 \log \frac{(\text{reductant})}{(\text{oxidant})} \text{ in volts.}$$

In this formulation, E_h is the potential difference between the standard normal hydrogen electrode and the system under examination. E_0 is a constant for the particular system under examination such that it equals E_h when reductant and oxidant are present in equal proportions and

$$\frac{(\text{reductant})}{(\text{oxidant})} = 1.$$

(R is the gas constant, T the absolute temperature, F the farad, and N the number of electrons involved in the particular reaction, e.g. *one* in the ferrous-ferric iron reaction. The brackets round the terms reductant and oxidant indicate the actual concentrations corrected for the "activity" of the reductant or oxidant.)

The fundamental point about this equation is thus that the potential of the system (E_h) is proportional to the logarithm of the ratio of reduced to oxidized products. This conception may be applied to all reversible oxidations and reductions studied, though irreversible reactions may involve other considerations. The potentials existing in such systems may then be termed oxidation-reduction potentials or, for simplicity, "redox" potentials, and the systems themselves are now often termed "redox" systems.

It is to be noted that the hydrogen ion itself may be regarded as an oxidation product in terms of this treatment. Thus:

$$H_2 = 2H^+ + 2 \text{ electrons}.$$

Here
$$E_h = -\frac{RT}{2F} \log_n \frac{[H_2]}{[H^+]^2}$$

$$= -0{\cdot}029 \,(\log [H^2] - 2 \log [H^+]) \text{ at } 20^\circ \text{ C}.$$

But $-\log [H^+]$ is equivalent to pH and Clarke has suggested that in a similar manner (see below) $-\log [H^2]$ should be designated rH, whence, at 20° C., the above equation can be expressed

$$rH = \frac{E_h}{0{\cdot}029} + 2\, pH.$$

The meaning of the term rH is as follows. It is possible theoretically to consider a redox system as one which is producing hydrogen by virtue of which reduction takes place. One measure of the intensity of reduction in such a system would be the pressure of hydrogen gas with which an electrode would be charged because of the reducing action of the system, assuming equilibrium to be reached. This cannot be measured directly and it must be assumed to be the pressure of hydrogen gas (in atmospheres) in equilibrium with a platinized electrode in a buffer solution of the same pH as the redox system, which gives the same potential as an indifferent electrode (e.g. bright platinum) without hydrogen gas in the redox system. The difference between this potential and that of an electrode of gas pressure equal to one atmosphere is proportional to $-\log [H_2]$, where $[H_2]$ represents the pressure of hydrogen in the example considered. It is this quantity which Clarke designated rH and it will be seen that it is a theoretical conception designed to express the intensity of reduction, or conversely of oxidation. Clarke now advocates that the use of the term be discontinued. In an actual example $rH = 0$ implies that theoretically the electrode is being charged with hydrogen at a pressure of one atmosphere. For $rH = 9$ the theoretical hydrogen pressure is equivalent to 10^{-9} atm. It will be noted that for higher rH values, e.g. $rH = 40$, the pressures are largely mathematical expressions.

The advantage of using the term rH lies mainly in the fact that the effect of pH upon the potential measured is eliminated. For this reason, the term has been frequently used in describing unknown and often mixed biological redox systems. In a similar way, it has obvious practical advantages in comparing, for example, soils of widely different pH values. Actually a known redox system is best described in terms of its E_h and pH. The use of the term rH makes the tacit assumption that there is a known simple relationship between the E_h and pH of the system of the type postulated above. It is possible to employ the same assumption without using the term rH, which is open to objection on account of its implications. The assumption is that each unit decrease of pH should be accompanied by an increase of E_h of 58 mV. (at 20° C.) as shown above. That the relationship is of this type in soil has been shown by the results of Willis (1932) and if this relationship is found to be general it would justify the comparison of soil potentials by adjustment to values calculated for a uniform pH. This procedure, which has been adopted

in this paper, avoids the use of the term rH, but it should be noted that the correction factor employed, 58 mV., may be too low. The relation between E_h and pH for inorganic soils as found by various authors (cf. Heintze, 1934) suggests a higher factor.

MEASUREMENT OF SOIL POTENTIALS

In practice the standard normal hydrogen electrode referred to in the development of these ideas is not usually employed. Generally and for soils, it is more convenient to use as the reference system a calomel electrode in which platinum wire dips into mercury below a layer of calomel-mercury amalgam. Above this is a solution saturated with calomel and potassium chloride. This is in contact with a saturated solution of potassium chloride which is connected by an agar bridge, also saturated with potassium chloride, to the system whose potential it is desired to measure. In this is also inserted a clean platinum (or gold) electrode. The calomel-potassium chloride-unknown system produces a potential (E) which is balanced against a known E.M.F. on a suitable potentiometer (e.g. Cambridge Instrument Co., Unipivot). A standard Weston cell may be used in accurate work for the known potential or to check the magnitude of another source of potential. With this arrangement the values of E in volts can be converted to the required E_h by

$$E_h = E + 0{\cdot}250 \text{ at } 20^\circ \text{ C.}$$

E in this expression will normally be positive for most soils and especially terrestrial soils, but in waterlogged soils it may be negative, necessitating the reversal of the connexions. The electrodes may tend to become polarized if left in contact with soil for a long time—and it is advisable to clean them frequently.

The advantage of the above arrangement in practice is that it can also be used for the measurement of hydrogen-ion concentration. In this case (and in our procedure) the soil is mixed with three times its volume of water and solid quinhydrone added. The whole is thoroughly mixed or shaken and the potential (x) measured. This will normally be of the same sign as that observed above. It may be converted to pH by the formula

$$p\text{H} = 7{\cdot}80 - \frac{x}{0{\cdot}058} \text{ at } 20^\circ \text{ C.}$$

Useful details about this latter method, the calomel and quinhydrone electrodes and the temperature corrections in these systems are given by Wright (1934). The results by this method are liable to distortion if manganese is present. The method suggested by Wright (1934) has been used as a routine check. The addition of a solution of quinhydrone should have no effect upon the colour given by suitable indicators with a soil suspension. Few suspicious soils have been encountered, but the readings for these and for alkaline soils have been done either with a hydrogen electrode or colorimetrically

Sampling and general procedure

There is in existence a number of papers dealing with measurements of soil redox potentials and a study of these shows that a remarkable variety of methods has been employed in preparing the soils for measurement. A large number of the measurements recorded have been made on air-dried soils, kept in a laboratory for some time and then suspended in water. Now while it may be true that each soil has its own redox potential under such conditions it seems that, ecologically at any rate, the potential existing in nature must be the significant one. Moreover, if we are really dealing in soils with reversible redox systems, it appears to be unlikely that the results obtained with air-dried soils will necessarily bear a simple relation to the potentials existing in nature. The evidence to be considered below suggests that storage and field conditions may well be widely different.

In attempting to measure the "natural" potential produced by a given soil, the addition of water is usually not necessary in dealing with north of England soils, though conceivably it might be so if very dry soils were encountered. Care is necessary, of course, to make sure that both the electrode and the agar bridge are in contact with the soil. When a soil is transported to the laboratory for potential measurements, very large drifts in potential may be observed in the course of a few hours. These can be shown to be affected by the closeness of packing of the soil sample, by the water content of the soil and also by the temperature at which it is kept. In order to compare these drifts with the original soil potential, although the apparatus is not readily transportable, a limited number of measurements have been made in the field. In these, a slit was made in the soil with a knife and a vertical plate electrode was inserted in this slit, the sides of the slit being pressed down to ensure a good contact. The glass carrying the agar bridge was inserted within 2 cm. of the electrode. Even this treatment caused some disturbance of the potential, and equilibrium was not restored until from 10 to 30 min. later. The potentials in the woodland soils examined fell slightly after the disturbance before becoming constant. After obtaining a constant potential the soil was opened up and a sample taken from the level of the electrode. Such samples were then taken to the laboratory and their potential drifts determined.

Some care is necessary in field observations in order to ensure that the electrode is in the required layer. In one case, four similar electrodes were put in within 10 cm. of one another. They gave final E_h values of (*a*) 380, (*b*) 440, (*c*) 530, (*d*) 535 mV. The ground was covered by *Deschampsia flexuosa* which forms a thick mat of live and decaying leaf bases below the foliage leaves. On opening up the soil (*a*) was found to be inserted in soft dead and rotting wood, (*b*) was in the leaf-bases mat, and both (*c*) and (*d*) were in the soil (rooting layer) beneath. The *p*H of this soil was 3·72.

In the first example to be considered, Table I, the soil sample, after the "field" determination, was divided into four parts. One of these, a piece retaining its original structure, was quickly weighed, placed in an oven at 95° C., and heated for 1 hr. It was then cooled, weighed again and sufficient distilled water was added to replace that lost by evaporation. Of the other samples one was a sample packed in a way used normally by shaking it down into the container and consolidating it lightly with the fingers. This was assumed to give a near approach to natural conditions, though actually the effect must vary with the soil texture. It is called "normal" packing. A third sample was closely packed and pressed down firmly by hand. The fourth sample was broken up into small crumbs and spread out on paper to give a large exposure to air. It was covered with a bell-jar to limit evaporation and half was used for potential measurement after 2 hr., the remainder after 2 days.

Table I. E_h *values in millivolts for a woodland soil, with much humus,* pH 4·03; *soil temperature*, 13·6° C.; *laboratory temperature*, 20–21° C.

Time in hr. ...	0*	2	6	24	48	96
1. Heated at 0·5° C.	495	480	500	514	494	503
2. Packed normally	495	596	655	644	630	615
3. Closely packed	495	550	445	458	480	505
4. Spread out in air	495	640	—	—	755	—

* Reading in nature.

These examples show that the drifts in potential in a sample of soil are largely controlled by the tightness of packing of the sample and, it may be assumed, by the degree of aeration. The fact that they disappear on strong heating suggests that the potential drifts are of bacterial or fungal origin. Similar results have been obtained with other samples and it is assumed that the phenomena are general.

It therefore seemed possible that the drifts might be prevented if a suitable antiseptic could be applied to the soil sample on collection. The type of antiseptic required would be one having no effect on soil pH and rH. Toluol appeared to fulfil all the conditions required, and its use appears to be generally a convenient method of maintaining the *status quo* of may soil samples. The sample is dropped into toluol in large crumbs 3–5 cm. in diameter, with the minimum disturbance and exposure to air.

Table II. E_h *values in millivolts of a woodland soil, with much humus,* pH 3·72; *soil temperature*, 13·9° C.

Time in hr. ...	0	1	3	18	24	48	72
1. Dropped into toluol	530	505	540	530	528	523	530
2. Dropped into distilled water	530	565	465	435	430	382	395
3. Packed normally	530	565	620	648	645	630	650
4. Closely packed	530	525	430	360	373	386	410

In Table II, examples are given showing the potential drifts observed after different treatments, in comparison with the values obtained by the toluol

treatment. Here again the original soil potential was observed in nature and the data refer to samples taken after this had been done, kept at a temperature of 19–21° C.

The table shows that in toluol the soil potential remains approximately constant, in marked contrast to its behaviour under other conditions of storage. There is a fall in potential of a similar order of magnitude in the closely packed sample and in that in distilled water. Here again then the results agree with the hypothesis that the drift in potential is of microfloral origin and also determined by the degree of aeration of the soil. It should follow from this that varying the water content will also affect the potential, as indeed is shown in the above example—and also in Table III below.

Table III. *Variations in* E_h *values due to changes in water content*—Vaccinium *soil*, pH 3·35; *temperature*, 13·8° C.

Time in hr. ...	0	1	3	24	48	72	96
1. Dropped into toluol	510	500	520	520	510	540	510
2. Saturated with water	510	595	570	530	460	435	480
3. Half saturated	510	555	590	570	550	540	540
4. No water added	510	530	620	620	630	645	640

The samples used in this series were stored at 20–21° C. and the zero reading is the "field" potential. They were all packed similarly in the normal manner although obviously the method of packing is not suitable to ensure absolute uniformity. Nevertheless, the results agree with others in showing that increasing the water content leads to different equilibria of potential. Further saturation of the soil with water normally leads to a fall in potential. This decrease was very clearly shown in a woodland soil of pH 7·71 taken from above magnesian limestone. This soil had been in the laboratory for 3 days at a temperature of 20–22° C., stored loosely in small crumbs in a stoppered bottle. It possessed approximately its optimum water content as judged by its texture and had reached equilibrium in its potential drift in air. Four similar samples were taken and packed as similarly as possible. One was kept unchanged, and one was just saturated with water, visible air being displaced. The other two had added to them respectively half and a quarter of the amount of water required to give saturation. An electrode was inserted in each. The potentials changed rapidly at first—but after 2 hr. they remained approximately constant. Taken in order of increasing water content, the E_h values were 455, 432, 399 and 342 mV., that is to say, that the potential decreased in inverse proportion to the rise in water content.

The examples given in detail in the tables refer to acid woodland soils, mainly because these soils were the only natural ones within a short distance of the laboratories where the work was done. Similar results have, however, been obtained for slightly acid or neutral soils, employing large blocks of soil quickly transported to the laboratory, for determinations of original potential. In all these cases, the drifts in potential were followed with the soil kept at

the laboratory temperature, or about 20° C., and undoubtedly the observed changes in potential are to some extent due to the higher temperature the soil assumes in the laboratory. The rate of change of potential in soils believed to be packed similarly is higher at higher temperatures and it seems probable that the final equilibrium may be different. Thus, in one case a block of woodland soil, *p*H 4·00, with an initial E_h of 480 mV. and a temperature of 14° C. gave an E_h of 510 mV. after 3 days at 13–14° C. and 655 mV. at 22° C. So much depends on the packing and other conditions affecting aeration that it is not possible to say that samples will always show a change of potential of the same direction when kept at different temperatures. Another sample of the above soil (actually collected after a period of heavy rain), with *p*H 4·05, showed a fall in potential from 465 to 370 mV. when kept at 13–14° C. and a rise of potential to 535 mV. when kept at 21–23° C. for 3 days. In both these cases, samples in toluol remained within 15 mV. of the original value.

It may perhaps be realized from these examples that it is not an easy matter to devise a method of carrying and packing samples which will maintain the potential met with in the field, though this could no doubt be done if the soil texture and temperature could be preserved unchanged. While the toluol method has proved useful in connexion with woodland soils in a dry or summer condition, it clearly has limitations. Experience shows that drifts of potential due to disturbance occur in damp or wet soils in toluol. Even woodland soils under the moister conditions prevalent in winter show large drifts of potential in the presence of toluol. One difficulty clearly is that the toluol cannot easily displace water held between the soil particles. Further, according to Lundegardh (1931), some soil organisms are able to oxidize toluol and Russell (1934) also refers to the possibility of ammonia being formed in soils treated with toluol. The toluol method, then, although the most useful at present available for small samples, is not altogether free fom suspicion.

Attempts have been made to see whether it was possible to use toluol for damper soils, by kneading samples from waterlogged soils underneath toluol so as to displace the water without admitting air. The kneading was done with a glass rod. The following example shows that this treatment may be fairly successful:

E_h *values of a waterlogged soil,* *p*H 5·56; *temperature,* 12·0° C., *kept at* 17–19° C.

Time in hr. ...	2	24	36	48
1. Kneaded under toluol	134	120	126	124
2. Dropped into toluol	126	85	76	68
3. Untreated	124	59	37	39
4. Water drained away, air present	137	198	218	202

The example shows that the potential is initially low in such a soil, a point which will be more fully discussed at a later stage. The drifts of potential are not stopped under toluol although much reduced by kneading below toluol.

As one might expect from the preceding examples, the potential falls on storing such a soil at a higher temperature, but rises if water is partly replaced by air.

The drifts in the observed potentials in this and the other examples cited agree with the view that these potentials are oxidation-reduction potentials. The effects of heat and of toluol agree with the assumption that the changes are at least accelerated by micro-organisms though they may not be wholly due to these organisms. Similar potentials were observed by Potter (1911) during the decay of organic manures. These points of view find further confirmation in the summary of data given below.

Comparison of potentials in different soils

Using the methods indicated above, a collection of estimates of soil potentials has been made which covers over 300 soil samples, representative of a wide range of soils under natural vegetation. These estimates are best considered in relation to their vegetation and this will be deferred until later papers. A general survey, however, brings out several points of interest and importance in the present connexion, and in illustration of these points a limited series of typical observations is given. These observations were all made either by transporting the apparatus into the field, or by rapidly transporting large and undisturbed blocks of soil to the laboratory for immediate estimation.

In order to make the estimates comparable, they are recalculated to obtain an estimated potential at *p*H 5 by increasing the observed value by 58 mV. for every decrease in *p*H of one unit or vice versa. Thus an observed value of 180 mV. at *p*H 6·0 would give an adjusted value at *p*H 5 of 238 mV. and a value of 250 mV. at *p*H 4 would give 192 mV. as the adjusted value at *p*H 5. The level of *p*H 5 is chosen for adjustment because this is about the average *p*H value of north of England soils under natural vegetation and also because, on the whole, it involves small adjustments to the observed potentials of certain soils whose potential levels appear to have a special significance.

The illustrative results in the table are arranged in groups according to their approximate water content. In the first group are the soils which were waterlogged at the time of examination. The second group comprises wet marsh or moss soils liable to complete submergence or waterlogging but not in this state at the time they were examined and in a normal summer condition. The third group includes a series of woodland soils, some damper, others drier. It will be seen from the table that in a general way the adjusted potential, E_5, increases as the proportion of water decreases and as the proportion of air increases. A waterlogged soil generally has a potential below 200 mV. (E_5). It is clear, however, from the examples of waterlogged soils alone that the potential is not wholly controlled by water and air content.

The effect of water content on potential (E_5) can be traced in detail on similar soils. Thus, of the *Salix cinerea* soils, No. 6 represents the driest, with

the water-level 15–20 cm. below the surface. In a similar manner, No. 11 had a water-level about 40 cm. below the surface, while for No. 12 the water-level was 15–20 cm. below the surface. Moreover, the E_5 value of No. 11 in January, when the water-level was near the surface, was only 75 mV.

Table IV. *Table illustrating variations in soil potentials*

No.	Vegetation	pH	E_h	E_5	Thiocyanate test: Alone	Thiocyanate test: $+H_2O_2$	Nitrate
1	*Carex inflata*	5·38	130	152	1	3	—
2	*C. inflata, Menyanthes*	5·47	155	182	1	2	—
3	*Myrica, Menyanthes, Sphagnum*	5·50	158	187	—	2	—
4	*Salix cinerea*	5·68	10	48	1	3	—
5	*S. cinerea*	5·49	135	163	1	3	—
6	*S. cinerea*	5·18	315	325	2	3	—
7	*Erica tetralix, Myrica, Sphagnum*	4·30	275	234	2	3	—
8	As 7 + *Calluna*	4·18	260	211	2	3	—
9	*Eriophorum vaginatum, Sphagnum*	3·85	355	288	1	2	—
10	*E. vaginatum, Erica tetralix*	3·81	345	276	1	2	—
11	*Spiraea Ulmaria, Phalaris arundinacea*	6·28	325	399	2	2	2
12	*Juncus sylvaticus*	5·08	355	360	2	2	1
13	*Molinia coerulea, Lythrum Salicaria*	6·01	300	358	3	3	1
14	*Teucrium Scorodonia*	4·35	505	467	3	3	2
15	*Pteridium aquilinum*	4·04	440	384	3	3	1
16	*Mercurialis perennis*	5·15	340	349	1	1	3
17	*Pteridium aquilinum*	4·54	445	418	2	2	1
18	*Brachypodium sylvaticum*	5·96	425	481	—	—	2
19	*Urtica dioica*	6·58	395	487	—	—	2
20	*Pteridium, Holcus mollis*	4·26	630	587	3	3	1
21	*Mercurialis perennis*	5·22	450	463	1	1	1
22	*M. perennis*	7·68	350	506	—	—	1
23	*Brachypodium sylvaticum*	7·21	370	498	—	—	3

Similarly, in the woodland soils, the first five represent estimates made on a transect across a small valley, the soil being similar throughout, a rather close-textured Silurian drift. Soil No. 18 (*Brachypodium*) was affected by detritus and drainage from a slaty outcrop and was on a steep slope. The *Pteridium* was on the gentler slopes and deeper soils, *Teucrium* at the top of the slope and *Mercurialis* in the hollow. The water and humus contents of the soils were as follows, the water/humus ratio being considered to give the best approximation to their relative humidities (cf. Crump, 1913).

Water and humus contents as percentage of dry weight

No.	Plant covering	Humus	Water	Water/humus
14	*Teucrium*	12·7	15·3	1·20
15	*Pteridium*	14·3	28·0	1·95
16	*Mercurialis*	11·3	41·5	3·67
17	*Pteridium*	14·7	30·0	2·04
18	*Brachypodium*	10·8	14·4	1·33

It will be seen that, here again, there appears to be a fairly definite relation between the E_5 value and the water content.

Of the remaining samples, No. 19 (*Urtica*) was also a Silurian drift, with numerous small stones, flushed by drainage from pastures, while the remainder

were Yorkshire examples. No. 20 (*Pteridium*) was an extremely open sandy leaf mould. No. 21 was a rather closely packed alluvial silt and Nos. 22 and 23 a fairly typical loam over Magnesian limestone. If difference of aeration due to differences of water content can cause differences in soil potential, then it is probable that similar variations in potential will originate from differences in soil texture. The last four examples in the table appear to exemplify mainly the effects of soil texture. They were done on the same day.

The wider range of North of England soils examined ranged in pH value from 3 to 8 and covered most natural vegetation and topographic types. The range of E_5 value lay normally between 0 and 600 mV. but in extreme cases values as low as -58 and as high as 700 have been recorded. (This corresponds to an rH range of 8–33.) The waterlogged soils examined have normally a value for E_5 below 250 mV. It does not follow, however, that a value below this means that the soil is saturated with water, several exceptions to this condition are known, all close-textured soils, some mainly mineral, others peats. On the present evidence, a soil below rH 200 would be expected to be saturated with water. Terrestrial (e.g. woodland) soils tend generally to be above E_5 380.

About 75% of the soils examined were deficient in bases as shown by Comber's thiocyanate test (1920). For this test, the soil is shaken with an alcoholic solution of ammonium thiocyanate. If the soil is deficient in calcium or other mono- or divalent ions excluding hydrogen, ferric iron is liberated from the resultant base exchange in quantities sufficient to produce a red coloration of ferric thiocyanate. Soils giving this reaction respond agriculturally to the addition of lime. Now it has been found by Dr R. Misra, in dealing with non-calcareous lake muds, that these muds gave little or no coloration with ammonium thiocyanate although subsequent leaching with ammonium chloride showed that they might be markedly deficient in such replaceable ions as calcium and magnesium. The iron in these muds was found to be in the ferrous state and their potential was low, usually below E_5 200. Exposure to air or oxidation with hydrogen peroxide, however, caused the oxidation of the iron to the ferric condition. The thiocyanate test was, therefore, modified in order to deal with these muds (Misra, 1937). After the preliminary treatment with ammonium thiocyanate the depth of colour was noted and 1 drop of hydrogen peroxide was added to each 10 c.c. of soil and solution. An immediate deepening of the colour showed the presence of ferrous iron and also enabled the existence of base deficiency to be demonstrated.

It may be observed that the modified test enables one to determine in base-deficient soils whether the replaceable iron is mainly ferric or whether a detectable amount of ferrous iron is also present. Since the ratio of ferrous to ferric iron should run parallel to the redox potential, it seemed of interest to determine whether any consistent connexion could be traced between the presence of ferrous iron by the modified thiocyanate test and the magnitude of the E_5 value. Hence we have applied the modified thiocyanate test to all

the soils examined. Above E_5 350, base-deficient soils give no visible increase in ferric thiocyanate colour after adding hydrogen peroxide. Below E_5 320 the base-deficient soils examined normally contain some ferrous iron and hence give an increased thiocyanate colour on adding peroxide. It should perhaps be noted that, in one limited class of highly organic peats, the colour reactions are difficult to observe, probably because of the low iron contents of these peats.

The type of result obtained is illustrated in the table of examples, the colour intensities obtained with thiocyanate being estimated visually at four degrees of intensity. The method in its present form is not sensitive enough to indicate exactly the ratio of ferrous to ferric iron in the soil, though there is a broad general agreement between the E_5 value and the results of the thiocyanate method when the visible differences are considerable. This is illustrated in the following table, where the samples were compared at the same time. In this table, A and B are two inorganic marsh soils with less than 20% of organic matter, while C and D were both peaty with more than 50% of organic matter.

	Intensity of colour with thiocyanate			
Soil	Without peroxide	With peroxide	E_5 (in mV.)	pH
A	0	4	119	5·51
B	2	3	299	5·13
C	0	3	160	5·38
D	2	3	258	4·91

When soils such as these, with E_5 below 320, are left in air, their potential rises above E_5 350, as shown in a previous example (p. 187), and at the same time the iron initially liberated in the thiocyanate test changes from the partly ferrous to the wholly ferric state. This change may be very rapid and may ensue in less than 24 hr. if the soils are well aerated. Here again, then, the evidence suggests that the transition occurs between E_5 320 and 350, and below this point the soils are reducing as indicated by the presence of ferrous iron.

It should be noted that the thiocyanate test is not necessarily a test of lime or base deficiency in such reducing soils. Ferrous iron is bivalent and will therefore be replaced (by ammonium ions) along with such ions as calcium and magnesium, not *after* them as is the ferric ion. Thus, in a calcareous mud (effervescing strongly with hydrochloric acid) from Malham Tarn (with E_5 243 and pH 7·46), considerable amounts of ferrous iron (colour intensity 2–3) were liberated, but no ferric. Several other similar examples have been noted.

Another interesting line of argument has been suggested by routine tests for the presence of nitrates in the soils examined. The test employed was as follows. Fresh soil was shaken with three times its volume of water and after 1 hr. 7 drops of 0·02% diphenylamine in concentrated sulphuric acid were added to 1 drop of the clear extract. The depth of the blue colour produced was noted, four degrees of intensity being used for recording. Soil organic

particles sometimes give this reaction and the absence of such particles from the test liquid is necessary. It appears from the results (as illustrated in Table IV) that nitrates are normally absent from soils of E_5 below 320 and conversely that soils containing nitrates have normally an E_5 value above 350. Further, in study of some of these soils, Misra (1937) has found that ammonium ions are relatively abundant, while the failure of nitrification in waterlogged soils is well known (Hesselman, 1917) and such soils, in our observations, have usually an E_5 below 300. Moreover, Darnell & Eisenmonger (1936) have studied a series of actively nitrifying soils to which lime had previously been added so that large changes in hydrogen-ion concentration had occurred. They concluded from their study that there was an apparent correlation between the magnitude of the soil potential and the logarithm of the ratio of nitrate to ammonia. In other words, a high potential implies a high ratio of nitrate to ammonia.

The possibility is not precluded with the diphenylamine reaction, that this substance is also an oxidation-reduction indicator, and the apparent nitrate reaction in soil extracts may be affected by this factor. We have, however, verified the presence or absence of nitrates in six typical soils, three above E_5 350 and three below E_5 300, by first distilling off ammonia from the filtered extract and then estimating nitrate after reduction with Devarda's alloy. The results agreed with the diphenylamine tests.

In our observations three exceptional soils have been observed which in nature contained nitrates and also had low E_5 values (170 to 26). In each case the soil was located in such a place that it was being flushed by stream or drainage waters containing nitrates. In one case the nitrate in the soil disappeared along the line of water movement after a distance of 30 m. from the source had been traversed. In another case the soil, after being kept in its waterlogged condition for 3 days in the laboratory, no longer gave its original weak nitrate reaction. Hence it seems evident that in such soils topographic features determine the inflow of nitrates, and that in such cases the presence of these salts is not necessarily indicative of the real soil properties.

We conclude from the facts summarized here that the soils examined undergo an alteration in properties in the vicinity of E_5 320–350, such that below that point products of reduction are demonstrable, while above it oxidation products are more prominent. It is, perhaps, not advisable at this stage, on account of the possibility of drifts in soil potential, to over-emphasize the exact point at which the transition takes place, and theoretical considerations suggest that this would be a *zone* rather than a point. If, however, the facts characteristic of the soils examined are of general application, it seems that soils below E_5 320 should be regarded as effectively reducing soils, while those above E_5 350 are predominantly oxidizing. Further, as the potentials calculated as E_5 values appear to agree broadly with other tests of the soil oxidizing and reducing properties, we are justified in the tentative assumption

that the potentials measured are oxidation-reduction potentials. The study of the drifts in these potentials and the evidence as to ammonia and nitrates both agree in pointing to the importance of the soil microflora and the degree of soil aeration in controlling these potentials. The use of these methods, therefore, seems to offer great possibilities either in comparing the activities of the soil microflora or in determining the effective aeration of different soils.

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THE SOIL COMPLEX IN RELATION TO PLANT COMMUNITIES

II. CHARACTERISTIC WOODLAND SOILS

By W. H. PEARSALL

(*With one Figure in the Text*)

This paper and its successor describe soils upon which certain characteristic plant communities in the north of England are found. The results appear to throw some light upon the nature of the soil complex as it is related to natural vegetation and hence may profitably be discussed as part of a general problem. A large proportion of the soils in northern England are acid and hence the special problems of acid soils figure most prominently in the discussion.

For convenience, the methods used may be summarized. They have been described fully in the earlier paper of this series (1938).

(1) The *p*H value of the soil is determined in quinhydrone saturated soil suspensions, the potential at a bright platinum electrode being measured against that of saturated potassium chloride solution and a saturated calomel electrode. Routine checks for the presence of manganese were employed and suspicious or alkaline soils determined with a hydrogen electrode or colorimetrically.

(2) The electrical potential of the soil is measured, and is assumed to represent the oxidation-reduction potential, with higher values indicating greater intensity of oxidation. The readings are given as E_h adjusted to *p*H 5 and called E_5. The adjustment is made on the assumption that an increase of unit *p*H will involve a decrease of 58 mV. in E_h. This correction may be too low (Pearsall, 1938).

(3) A base-deficient soil is considered to be one giving a red coloration with Comber's thiocyanate reaction. The depth of colour produced is shown in the tables by figures varying from 1 to 4. An intensification of colour on the addition of hydrogen peroxide to the clear liquid after this reaction is used to detect replaceable ferrous iron (Misra in paper I). The final depth of colour under these conditions is shown as the second numeral in the tables. Thus 1/3 indicates an intensity of 1 with Comber's test and 3 after adding the peroxide.

(4) Calcareous soils are defined as those effervescing with dilute hydrochloric acid (33 %).

(5) The intensity of colour (1–4) produced on adding to clear extract of the soil 0·02 % diphenylamine in concentrated sulphuric acid is used for estimating nitrates.

The results given in this paper are all for samples of soil collected in July, August and September. The reasons for confining the observations to this period were two. In the first place, it was desired to compare soils from bogs and marshes with those from woodlands. The vegetation of the former habitats is comparatively late in development, and, moreover, later in reaching the summer equilibrium. Secondly, nitrate tests on fresh soil are at times negative when plants are actively growing, as absorption may equal the rate of production. This difficulty is not usually encountered in full summer conditions. It is true that it may be overcome by other methods. Thus Olsen (1921) left the soils for 10 days before carrying out nitrate estimations. This procedure is useful at times with doubtful soils, but it should be realized that the soil has been thoroughly disturbed in sampling and air has been admitted. The presence of nitrates after 10 days in the laboratory is no proof that they were present in nature (cf. Olsen's soil, No. 15), and indeed examples have been recorded in which strongly reducing soils produced nitrates after exposure in air. Similar arguments apply to measurements of oxidation-reduction potentials and even to tests for ferrous iron (Pearsall, 1938). It has, therefore, been the rule in this work to examine the soil with as little disturbance as possible, and many of the measurements (shown with an asterisk in the tables) were done in the field. Samples for laboratory measurements were either soaked in toluol (marked by *t* in the tables) or taken in large blocks (of which the centre was used) and with precautions against changes of temperature.

Lastly, the soils examined were chosen on the basis of their vegetation and the samples were confined to the characteristic plant communities of the areas investigated. Lists were made of the plants present within half a metre of the sampling place. These lists are not given in detail as the community described is usually adequately indicated by the name of its dominant. In choosing areas for sampling preference was often given to those containing tree seedlings but the essential condition was that the plant community should be representative of a considerable area. Transitional examples were not taken. So far as it is possible to say, the samples refer to areas which show no signs of having been recently modified by man or grazing animals. The terrestrial soils to be considered below are those of woodland plant communities. Grasslands are not considered in detail largely because their composition seems to vary with grazing pressure. The woodland communities are mainly those found in the Lake District on Silurian rocks (slates or grits), and those found in Yorkshire, especially near Leeds on carboniferous grits and sandstones or on magnesian limestone. The necessity for immediate determinations of potential has limited the areas under observation. The range of woodland vegetation in these areas varies very considerably. In Yorkshire, the vegetation on the sandstones and grits centres round the *Holcus mollis-Scilla nonscripta-Pteridium aquilinum* community. Of these three plants, *Pteridium* with a habitat range known to be very wide, is unsuitable as an indicator plant,

Scilla is often difficult to find in late summer and both suffer from the disadvantage for this type of work of being comparatively deep rooted. Consequently, *Holcus* has been used as the indicator plant. In these woods, *Deschampsia flexuosa* is the other common plant, forming practically pure communities, and a dense mat of leaf bases. *Milium effusum* often forms extensive communities towards the base of slopes and where the water content is higher. Neither of these plants has any frequently present associates in the small areas examined. The Lake District soils of similar type are rarely covered by closed ground flora communities. There is a general oakwood community of a rather open type which tends to approach one of three extremes. *Pteridium aquilinum* may also be present wherever the light intensity is sufficiently high, more than 20%, and the soil sufficiently deep, over about 20 cm. The three extremes tend to have (*a*) *Teucrium scorodonia*, (*b*) *Deschampsia flexuosa*, or (*c*) *Agrostis vulgaris* and *Anthoxanthum odoratum* as most abundant plants, with a fair amount of exposed soil and similar subordinate associates. In the examples cited in this work (table in Appendix), the following species occurred in more than 30% of the quadrats. The attached figure gives the percentage of quadrats in which the species was observed.

Teucrium scorodonia	76	Agrostis vulgaris	36
Pteridium aquilinum	60	Anthoxanthum odoratum	32
Oxalis acetosella	56	Lonicera periclymenum	36
Deschampsia flexuosa	56	Lychnis dioica	36
Galium saxatile	42	Hypnum cupressiforme	42
Potentilla erecta	36	Catharinea undulata	32

Galium saxatile shows a marked correlation in distribution with *Deschampsia flexuosa*. It should especially be realized that the examples cited with *D. flexuosa* abundant do not resemble at all the *D. flexuosa* community of the Pennine areas, as on an average nine species are present in each quadrat.

A summary of the results for woodland soils is given in Table I, the actual details being presented in tables in the Appendix. Some of the data there are not included in the list of plant communities given in the summary.

Table I

Community	No. of samples	pH	E_5	Thio-cyanate	Ni-trate	Seedlings
Vaccinium Myrtillus	8	2·87–3·59	382–482	2–3	—	5*B*, 1*Pa*
Deschampsia flexuosa	9	3·32–3·80	416–506	3–4	—	2*B*, 1*Pa*
Dicranum majus	6	3·38–3·85†	345–465	1–4	—†	1*B*, 1*Pa*, 1*Q*†
Holcus mollis	9	3·86–5·29	422–507	1–3	1–3	5*Q*
Milium effusum	4	4·05–5·06	410–465	1–3	2	2*Q*
Lake District	13	3·87‡–5·32	408–527	1–4	1–3	3*A*, 3*A*, 1*B*, 1*Pa*, 1*T*
Brachypodium sylvaticum	12	5·15–7·40	480–580	0–2	1–4	6*F*, 3*Q*, 1*A*
Mercurialis perennis	8	5·15–7·80	434–525	0–2	1–3	5*F*, 1*U*

† See No. 79. ‡ Excluding No. 69.

(Seedlings: *B*, *Betula* (usually *pubescens*); *Pa*, *Pyrus aucuparia*; *Q*, *Quercus*; *A*, *Acer pseudoplatanus*; *T*, *Taxus*; *F*, *Fraxinus excelsior*; *U*, *Ulmus montana* St.)

On the basis of the soil properties, the plant communities studied fall into three main groups as follows:

(A) *Vaccinium*, *Deschampsia* and *Dicranum*, normally on soils which are base deficient, and *below* pH 3·8 with nitrates absent. Earthworms not observed.

(B) *Holcus*, *Milium* and general Lake District type, normally on base deficient soils *above* pH 3·8, and below (approximately) pH 5·0–5·3. Nitrates always present, earthworms observed.

(C) *Mercurialis* and *Brachypodium* on soils often calcareous, at times base deficient, above pH 5·1 (approximately). Nitrates present and earthworms observed, in moister examples particularly.

In general, the soil types so distinguished correspond to the distribution of tree seedlings. Thus *Betula* and *Pyrus aucuparia* predominate on soils of class A, *Quercus* on soils of class B and *Fraxinus* on soils of class C. The single oak seedling recorded for class A came from a soil of border-line properties (No. 79), pH 3·85 with nitrates present. In a general way the soils of class B are those of oakwoods, and those of class C of ashwoods or of ash "streaks" in oakwoods. But because the soil was sampled for ground flora species (rooting level) no exact relation can be expected to hold between the soils and the mature trees. Data are given for the underlying drift in the Lake District (Nos. 73–75) which probably represent the rooting layers of these oakwoods.

The magnitudes of the potentials, E_5, shows that all these soils are oxidizing, also shown by the absence of ferrous iron with the thiocyanate test. *Milium* and *Mercurialis* tend on the whole to occur on damper siliceous soils than *Holcus* and *Brachypodium* respectively and the soils tend to range towards lower potentials. The damper soils tend to have closer texture and this along with their high water content might be expected to reduce aeration and oxidation intensity, though these effects would clearly be at a minimum in summer. The higher oxidation potentials of the *Brachypodium* soils are noteworthy in comparison with the high values for nitrates recorded.

The potentials are of most interest in the most acid soil group. *Dicranum majus* and *Vaccinium* both occur with a lower range of soil potential than *Deschampsia flexuosa*. *Dicranum* tends to replace *Deschampsia* in the Lake District, and it appears possible that the more humid climate is responsible for this and hence that the mosses may occur on less well-aerated soils. The closeness of the moss carpet would doubtless contribute to this.

The fact that all of this group of acid soils shows high oxidation intensity is of great interest, for it implies that oxygen must be present in amounts sufficient to facilitate to the soil oxidation processes, although the lower potential range in the *Vaccinium* and *Dicranum* soils suggests that diffusion of air into the soils may be relatively slow. No doubt the high organic content of these soils, over 85% in the samples taken, will also tend to imply a low

ratio of oxygen to organic matter and hence possibly a lower oxidation intensity. The absence of nitrates in these soils is not, however, due to deficiency of oxygen but to other causes. The remarkable feature of the results is the definite boundary at *p*H 3·8 below which nitrates disappear, though it will be seen later (in the second class of damp woodland soils) that this boundary is not always so sharp. Extensive data given by Heimburger (1934) for forest soils in the Adirondacks also show that there, nitrifying organisms are normally only present when the *p*H is above 3·8–4·0. Heimburger does not draw any conclusion on this point however. His method, a modification of that of Winogradsky, does not record the intensity of nitrification in undisturbed soil.

The classification of soil types given here bears obvious resemblances to the biological classification suggested by Muller (1887) and Hesselman, who distinguished two main types of forest soils, *mull* and *mor*, (or torf). In extremes, *mull* is a well-aerated soil containing nitrates and bearing vegetation often including nitratophilous species. The humus tends to be of the open "leaf mould" type and earthworms are normally present. *Mor* on the other hand, normally lacks both earthworms and nitrates and commonly includes in its vegetation ericaceous species or plants of a similar ecological type. Because of the absence of earthworms and nitrates, *mor* was originally supposed to be badly aerated if not quite devoid of oxygen. These conceptions of soil types have proved of great value in forestry silviculture. Thus, for example, beech is known to regenerate on *mull* but not on *mor*.

This is not the place to review the extensive literature dealing with these soil types, but two points seem to be worthy of emphasis. Much of the confusion which has arisen as a result of attempts to apply this nomenclature may have arisen from the failure to study the soil as it is in nature. An organic soil removed to the laboratory often possesses quite different properties from those it shows in its natural condition. Secondly, this classification is primarily biological and this point of view requires further attention.

Romell (1932, 1935) has stated very clearly the recent arguments for regarding *mull* and *mor* as representing biological systems. His papers should be consulted by all interested in these questions. He has shown that there is no marked deficiency of oxygen in *mor* and he pictures the difference between this and *mull* as being due largely to differences in the micro-organisms present. Thus, while *mull* contains large numbers of aerobic bacteria whose jelly capsules constitute a significant part of the humus colloids, *mor* contains predominantly fungal hyphae, especially Hymenomycetes and often mycorrhizal organisms. Thus the real difference between *mull* and *mor* lies not necessarily in the existence of different *rates* of activity, but in the presence of different *kinds* of decomposition and probably of different types of resynthesis of the organic products of decay. Running parallel with these distinctions are differences in the soil fauna, though these appear to be less thoroughly known.

Romell, however, suggests that *mull* represents a delicate dynamic equilibrium in which the soil fauna plays an important part in destroying the soil fungi. *Mor*, however, tends to be self stable unless disturbed.

This bare outline does not do justice to the information available about these two soil types but it contains sufficient to enable us to consider the results obtained in this survey. Undoubtedly, the woodland soil type below *p*H 3·8 may be regarded as *mor*. The soils above this *p*H level are regarded here as *mull*, though it is probable that they must include soils which are transitional to *mor*. No certain method of distinguishing the latter transitional soils has yet been evolved, though *Deschampsia flexuosa* is regarded as a useful indicator species in this respect (see Nos. 67–69). The wide range of soil *p*H covered by such species as *Urtica dioica* (Nos. 56–58 and Olsen, 1921) on soils which have a characteristic *mull* appearance, tends to show that the *p*H range of *mull* is wide, and includes both of the less acid soil types distinguished here. The rather indefinite nature of the *p*H boundary about *p*H 5 tends to suggest also that the soil types distinguished here are not necessarily very distinct, and a wider range of soils derived from different rock formations would possibly show a bigger overlap at this point. Romell (1935), however, states that when stored *mor* becomes more acid and *mull* less acid, though he also states that his observations on this point have been scattered. I have not been able to satisfy myself on this point and suspect that a good deal of variation exists in changes of acidity depending upon the conditions of storage. The question might well be fundamental as the moulds are assumed to be the main acid-producing organisms. The only evidence offered here (see below), while certainly true for the six soils examined, is not considered to be certainly representative.

Since the question of the character of different soil types depends very greatly on the type and quality of their activities, a good many efforts have been made to devise methods of measuring soil activity. A general criticism of these methods, so far as my experience of them goes, is that they measure activity as shown in the soil kept under laboratory (and quite different) conditions. If this view is justified, then the ideal measure of activity ought to be on the soil maintained under conditions as nearly as possible those found in nature. There are obvious practical difficulties in doing this. The method of attacking the problem used in this work has been to make use of the rapid changes in oxidation-reduction potential observed in disturbing a soil (Part I). In theory, if a soil is thoroughly exposed to air, the final potential would probably always tend to approach a constant value, while the rate of change would depend upon such factors as the degree of aeration and the number of oxidizing organisms present. Because the degree of aeration cannot easily be adjusted to a similar level in different soils, this method appears to give somewhat variable results, though they resemble those obtained below by an alternative method. In this, samples of soil collected as carefully as possible

to avoid structural change, were transported to the laboratory and exposed to a higher temperature. A spade electrode was inserted with the minimum disturbance, the soil pressed down round it, and the potential measured at intervals. The electrode (2 cm. long) was 4–6 cm. below the surface. The *p*H values are also from samples taken from below the surface. The soils were all between 13 and 14° C. when collected and they were kept at 22° C. It is to be noted that there was no vegetation on the sample surface and no resistance to the diffusion of air, except that due to the soil texture. The results are given below for two soils of each of the three main soil types recognized.

Table II. *Changes of potential and* pH *in soils of different types*

Community	E_h at stated time in hr. 0	12	24	48	Change of E_h 24 hr.	*p*H Initial	48 hr.
Brachypodium	320	405	450	490	130	7·11	7·42
Mercurialis	420	480	520	545	100	4·98	5·19
Holcus	570	620	630	635	60	3·90	3·77
Milium	515	555	580	590	65	4·32	4·20
Deschampsia	545	640	665	660	120	3·60	3·43
Vaccinium	520	600	645	665	125	3·27	3·15

The data show that each pair of soils behaves in a similar manner. The rate of change in potential E_h (i.e. not corrected for *p*H) is high in the least acid soils and in the most acid ones, but relatively low in the *Milium* and *Holcus* samples. One explanation of this would be that the latter soils are least active in oxidation and they might thus contain fewest oxidizing organisms. The alternative possibility would be that they are already highly oxidized, so that the possible drift under these conditions is less. The observed initial potentials, recalculated to *p*H 5, agree broadly with this hypothesis as the initial E_5 values were in the same order as the table: 442, 419; 506, 476; 464, 420. From this point of view, the soils with larger potential drifts would be those into which air diffused more slowly so that the initial potential (E_5) was lower and the drifts continued for a longer time, which appears to be true.

The data also show that the *Holcus* and *Milium* soils resemble the most acid ones in showing an increase of acidity *under these conditions*. An allowance of *p*H 0·1 must be considered as representing the extreme possible variation in measurement, and hence the results appear to be significant. They are certainly reproducible for these six soils, and confirm Romell's statement about the increased acidity of *mor* on storing. It seems probable, however, that a wide examination of the effect of storage conditions upon these changes will be necessary before generalizations can safely be made.

Woodland soils of aquatic origin

Necessarily included in the woodland soils, but involving an additional set of problems, are the woodland soils which have been derived from aquatic habitats. The additional problems partly result from waterlogging, which

may result in scarcity or absence of oxygen. Such soils (see Part I) have low E_5 potentials and no nitrates, while ferrous iron is present. These soils are termed *reducing* soils. But the soil types now to be considered are also usually parts of developmental series and show high rates of change, and so in practice they can only profitably be considered in their developmental sequences. The discussion will thus be limited for the present to examples in which these sequences can be inferred.

Birchwoods, however (containing more than 60% of birch), also occur on peats of aquatic origin. These appear to form a distinctive and stable type of soil (Nos. 83–94) which is not different in any observed particular from the soil of upland birchwoods (Nos. 3, 4, 15, 16, 92). The soils are strongly oxidizing and, whatever their origin, do not appear to differ from *mor* as previously defined. Two additional ground flora communities occur, dominated respectively by *Molinia coerulea* and *Dryopteris dilatata*, the latter usually with *Oxalis acetosella* and *Mnium hornum*. The ecological relations of the various ground flora communities are not fully worked out. While the soil characters of birchwoods on deep peats thus fall into place in the scheme for purely terrestrial soils, it should be noted that all the birchwoods of this type we have been able to find show clear evidence of artificial drainage.

Only one detailed example of an alderwood is given, this being the only one observed in which developmental sequences could be traced. This wood (Stable Hills) is developed on inorganic silts deposited by a small stream running into Derwentwater.

The examples in the table start from a *Phragmites* reedswamp near the mouth of the stream (No. 93) and include two examples in order of age of the mixed willow wood developing from this swamp. The succeeding examples of alderwood on inorganic silts are taken in succession until the point farthest from the lake and stream mouth is reached. The stream is occasionally subject to very violent floods when it brings down gravel. In one well-defined area, the soil is gravelly or drained by a gravel layer beneath. Here the mixed willow stage has developed into ashwood—exemplified by Nos. 102, 103. Both possible successions are topographic, in the sense that they are initially determined by the type of sedimentation, and the raising of the soil level is chiefly due to this cause. The pH of the soil, low when soil and water levels coincide (No. 93), rises to 7·14 by the time flooding has become scarce (No. 95). *Salices decipiens*, *cinerea*, *viminalis* and *fragilis* are all frequent here along with alder and ash. During this phase the soil changes rapidly from a strongly reducing one to a strongly oxidizing one, as the summer level rises above water level. When this mixed wood gives rise to ashwood, the soil characters are not distinguishable in summer from those of the general ashwood type already described. The soils of the alderwood (on silt), however, show a lower range of potential, though they are, in summer, all oxidizing as judged by the criteria available. The chief feature of interest is the remarkable fall in pH they show

from an initial value of over 7 to a final stage, where *Betula pubescens* is abundant (30%) when the pH value is near 4·0. In this wood, these acid soils (Nos. 98–100) are marked by the appearance of a layer of peat apparently mainly derived from fern detritus, and when this is fully developed (No. 100) the potential shows a marked fall. The general drift is shown by an arrow in Fig. 1.

Similar in its general features, but showing far less extreme variations, is the series of samples (Nos. 103–109) taken along the zone of most rapid silting in the North Fen (Esthwaite Water) previously described in this *Journal*

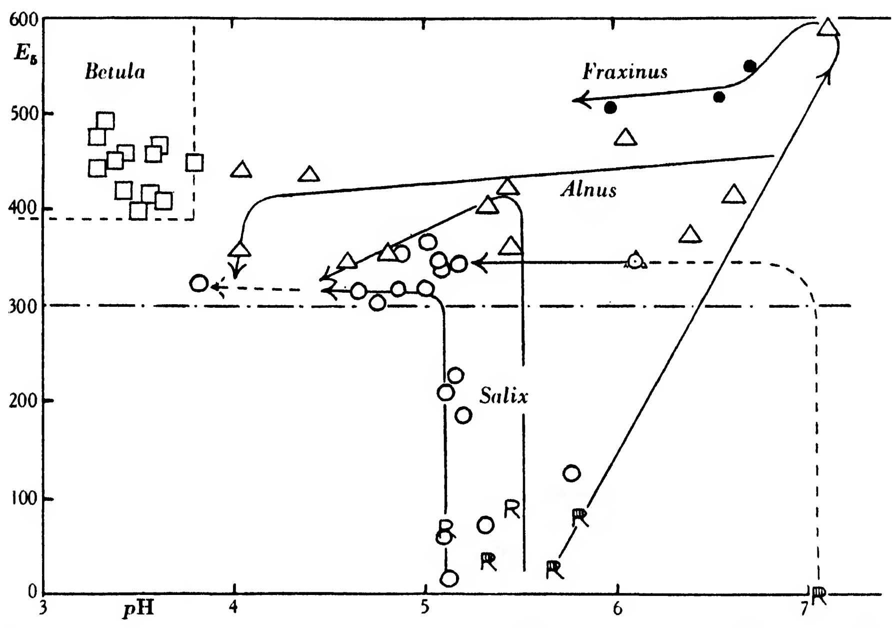

FIG. 1. Data for oxidation-reduction potential and pH value of damp woodlands, showing observed successions by continuous lines, possible successions by broken lines. The symbols used are (1) *Salix cinerea* series—circles. (2) Mixed willow and *Alnus*—triangles. (3) *Betula*, over 60%—squares. (4) Reed-swamp—R, shaded loop indicating *Alnus* series.

(1918). Most of the bushes on this zone have been now removed, but *Alnus* is still the most frequent tree, and the area represents an alderwood probably of a transitional type. Here again the samples farthest from the open water show both a fall in pH and in potential. It is worth while noting at this point that the thing which distinguishes the soils of these alderwoods from the soils of oak or ashwoods at the same pH is not the summer readings of potential, but those in winter or in flood periods. All the Esthwaite soils described with a potential E_5 of 350–420 in summer had E_5 potentials below 300 in January, even although the water levels were low at the time of sampling. The values observed at marked localities are noted in the table Nos. 105–107. Similar

results are available for the Stable Hills wood, by the ferrous-iron test. In winter, then, these soils tend to possess reducing properties, and nitrates are absent unless washed in by the stream.

The last type of woodland considered here is dominated by *Salix cinerea*, and in this case the soils differ from all others in both their low potential and the approximately constant *p*H (5·3–4·7) during development. These are, moreover, all more or less peaty soils (see Pearsall, 1918). The examples from the North Fen at Esthwaite Water (Nos. 110–118) again represent a successional series from reedswamp to the oldest part of the wood. The three "young" examples lie in wood which has developed since 1914. In all of these cases, the soil is waterlogged and the E_5 potential is accordingly low and nitrates are absent. The chief changes in the older parts of the wood are that *p*H falls to just below 5, while the potential rises and approaches E_5 300–320. The examples from Rusland and Brother's Water are essentially similar, although one of the former (No. 122) and all of the latter have somewhat higher E_5 values, possibly due to the presence of a few shallow artificial drains. (The aberrant example No. 126 in this series was for a station with underlying gravel, flushed by a stream and with a good number of ash trees and seedlings present.) The last examples (Nos. 127–132) differ from the others in being taken from places where the ground waters are calcareous, Roudsea Tarn (N. Lancs) and Malham Tarn (W. Yorks.). The former wood is of a transitional type with 24% of *Alnus* and some birch. The Malham Tarn example is interesting as including a state in which the willows were all dead or dying (No. 129). The high acidity in this case may be partly due to drainage from an adjacent peat bog, but the two earlier samples fall exactly among the Esthwaite series and the most acid one lies in the direction in which the Esthwaite series appears to be developing.

The general conclusion drawn from these examples is that *Salix cinerea* woods normally occur on reducing soils in the area studied. During the development of these woods, the soils possess *p*H values between 5·1 and 5·5. When the soil approaches the level at which oxidation of ferrous iron is possible and when nitrates may appear, its *p*H tends to fall below 5 and *Betula pubescens* appears (not more than 30%), while *Frangula Alnus* is also normally present and may be as abundant as *Betula* (cf. Rusland, Nos. 121, 122). Dying *Salix cinerea* has been seen at *p*H values of 4·40 and 3·82 and we have no other records of this species below 4·5. It appears to colonize only above *p*H 5·1 or 5·2.

In order to simplify the comparison of these results, the main observed lines of succession for alder and willow woods are given in Fig. 1, the arrows indicating the successional sequence of the various series and the points the observations. The striking feature of the various alder and willow successions observed is that they all tend to progress to a zone between *p*H 4 and 4·6 with an E_5 potential of between 300 and 350, that is approximately on the border

line between oxidizing and reducing soils. Since these data are mainly for summer, it must follow that most of these soils, and certainly those with *S. cinerea* as the dominant, must be reducing soils for the most of the year. Hence the plant communities succeeding these willow woods must be communities tolerating this type of soil. While it is possible that birchwoods may grow on such soils, we have so far been unable to find any examples which do. All the birchwoods examined grow on soils with an E_5 potential above 400 in summer. Thus it seems probable that, unless birch is exceptionally efficient in increasing soil drainage, birchwoods can only arise from *S. cinerea* woods after drainage. This may be true also for alderwoods though additional examples of these are required.

An additional point worthy of notice is that while these wet soils have a potential (E_5) below 300, no marked reduction of pH apparently takes place. Above this potential, however, downward drifts of pH appear. This is interpreted as meaning that soil oxidations producing organic acids (and presumably brought about by moulds or similar fungi) are not possible until this oxidation-reduction potential is reached. Presumably this potential level corresponds to that at which some oxygen can diffuse into the soil at some time during the summer months.

Finally, the data included here substantiate those given in the earlier paper of this series (1938) in showing that the presence of ferrous iron can be demonstrated at a potential below about 340 while above this point nitrates are normally present, if the soil pH exceeds 3·8. Two types of nitrate deficient soils are therefore recognized, one a reducing soil characterized by *S. cinerea* woods (or by swamps) and the other the oxidizing soils below pH 3·8, characterized by birch, birch-oak or birch-pine woods. The soil types found between pH 4 and 5 seem to be of a transitional nature and the zone near pH 5 seems to possess a special significance in relation to vegetation types, as, both in purely terrestrial woods and in those developed from hydroseres, a change in the vegetation usually appears below this point.

In conclusion, the data seem to justify the view that the plant communities in these areas bear a definite relation to soil conditions. They also suggest a basis for the classification of natural soil types.

Summary

On the basis of the distribution of natural types of woodland vegetation in northern England in relation to soil characters, five soil types are tentatively recognized.

Oxidizing soils

1. Base deficient soils lacking nitrates and with a pH below 3·8 in this area. Characterized by communities of *Vaccinium Myrtillus, Dicranum majus, Deschampsia flexuosa*, birchwoods, and birch seedlings.

2. Base-deficient woodland soils (usually oakwoods) between pH 3·8 and 5·0 (approx.), with nitrates (and earthworms) normally present. Characterized by *Holcus mollis* and *Milium effusum* and general oakwood (defined) communities with oak seedlings.

3. Woodland soils above pH 5·0 (approx.) with nitrates present, calcareous to slightly base deficient, characterized by *Mercurialis perennis*, *Brachypodium sylvaticum* communities and ash seedlings.

4. Soils oxidizing *in summer* tending to be reducing in winter, pH above 3·8, nitrates present in summer. Characterized by *Alnus glutinosa* woods and probably by *Phalaris arundinacea* and *Spiraea ulmaria* communities.

5. *Reducing soils*, pH tending to be above 5, nitrates absent, characterized by *Salix cinerea* woods.

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APPENDIX

The detailed results are given in the following tables. The symbols employed are described earlier in the paper except as follows. Localities in Yorkshire are shown by (Y), all others being in the Lake District. The ground flora species are shown either as abundant, a., or frequent, no sign. The symbols for seedlings are given in the text, Table I. In the column for remarks may be given the dominant tree, the height of the locality in m. (e.g. 300 m.) or numbers representing the percentages of different tree species present. The headings of each *group* of results indicate the dominant species, additional noteworthy species may be shown for each entry. Under the heading thiocyanate, *ca.* indicates a calcareous soil.

	Place	Ground flora	pH	E_5	Thio-cyanate	Nitrate	Seedlings and Remarks
			Vaccinium Myrtillus				
1.	Wyke (Y)	—	3·17	414*	2	—	*B.* Oak-birch wood
2.	Norwood Edge (Y)	—	3·23	396 *t*	3	—	*B.* Oak-birch, 300 m.
3.	Adel (Y)	—	3·31	482	2	—	Birch scrub
4.	Adel Moor (Y)	—	3·59	456 *t*	3	—	*B.* Birch scrub
5.	Wray	*Polytrichum commune*	3·51	471*	2	—	Oakwood
6.	Red Nab	*Deschampsia flexuosa*	3·42	440	3	—	*B, Pa.* Oakwood knoll
7.	Deerdyke	*Bracythecium purum*	2·87	382 *t*	2	—	Pine = birch
8.	Bortree	*Plagiothecium undulatum*	3·56	436 *t*	2	—	*B.* Oak-yew-birch
			Deschampsia flexuosa (Yorkshire)				
9.	Long Causeway	—	3·68	506	3	—	Oakwood
10.	,,	—	3·80	448 *t*	3	—	*B.* Oakwood
11.	Meanwood	—	3·49	495*	3	—	Oakwood
12.	,,	—	3·56	457 *t*	4	—	Oakwood
13.	Weetwood	—	3·63	454*	3	—	Oakwood
14.	Norwood Edge	—	3·53	518	4	—	*B.* Oak-birch, 300 m.
15.	Hawksworth	—	3·60	462 *t*	3	—	Birch, 270 m.
16.	Eccup	*Agrostis vulgaris*	3·56	416 *t*	3	—	Birch, 240 m.
17.	Ilkley	*Plagiothecium sylvaticum*	3·32	460 *t*	3	—	*Pa.* Oak-birch, 240 m.
			Holcus mollis (Oakwood, Yorkshire)				
18.	Arthington	*Scilla, Pteridium*	4·26	443*	3	1	*Q.* Worms
19.	,,	*Scilla, Pteridium*	4·12	450 *t*	3	2	Base of slope
20.	,,	*Pteridium*	3·86	466 *t*	3	1	*Q.* Top of slope
21.	Weetwood	*Scilla*	3·89	498*	3	1	*Q.* Worms
22.	,,	—	3·94	465 *t*	3	1	*Q*
23.	Harewood	*Scilla, Pteridium*	4·01	507	3	3	Worms
24.	Spofforth	*Pteridium, Teucrium*	5·29	422	1	1	Sandy—little humus
25.	Plumpton	*Teucrium, Lychnis dioica*	4·57	—	2	2	*Q.* As 24
26.	Tholthorpe	*Pteridium, Lonicera*	3·96	489 *t*	3	1	—
			Milium effusum (Yorkshire)				
27.	Weetwood	—	4·32	436 *t*	2	2	Worms
28.	,,	—	4·05	465	3	2	*Q.* Worms
29.	Arthington	*Oxalis*	4·29	410 *t*	2	2	—
30.	,,	*Lychnis, Brachypodium*	5·06	—	1	2	*Q*
			Mercurialis perennis				
31.	Arthington (Y)	*Nepeta hederacea, Eurhynchium striatum*	7·20	509*	*ca.*	2	Calcareous
32.	,,	*Eurhynchium praelongum*	5·75	459 *t*	1	2	—
33.	Moss Carr (Y)	*Conopodium denudatum*	5·09	434 *t*	2	1	Alluvium
34.	,,	*C. denudatum*	6·56	—	0	2	*U*
35.	Bardsey (Y)	*Hedera helix*	7·85	524 *t*	*ca.*	2	*F.* Worms, Magnesian limestone
36.	Wray	—	7·12	525*	0	2	*F.* Worms
37.	Cunsey	*Eurhynchium praelongum*	5·98	439	0	1	*F.* Worms
38.	Roudsea	*Geum urbanum, Mnium undulatum*	7·37	471	*ca.*	2	*F*
39.	Sawrey	*Adoxa, Catharinea undulata*	5·15	483	1	3	*F*

			Brachypodium sylvaticum					
40.	Fosse Bridge (Y)	*Arum maculatum*	5·52	—	2	4	*Q.* Alluvium	
41.	,,	*Dactylis, Rubus idaeus*	5·68	—	1	4	Alluvium	
42.	Moss Carr (Y)	—	5·47	479	1	3	*F.* Alluvium, worms	
43.	,,	*Sanicula europea, Geum urbanum*	6·80	520	*ca.*	3	*F.* Alluvium	
44.	Bardsey (Y)	*Geum urbanum*	7·40	509 *t*	*ca.*	2	*A.* Worms	
45.	Alne (Y)	—	4·84	494	2	3	*F*	
46.	Tollerton (Y)	*Urtica, Oxalis*	4·70	512	2	4	*Q.* Worms	
47.	Grass Wood (Y)	*Deschampsia caespitosa*	7·35	580 *t*	*ca.*	3		—
48.	Wray	*D. caespitosa*	6·14	515*	0	2	*F.* Worms. Flush	
49.	,,	*Eurhynchium praelongum*	6·98	520*	0	3	*F.* Flush	
50.	Red Nab	*Sanicula, Rubus idaeus*	5·96	480	0	1	*F.* Worms. Flush	
51.	Yewdale	*Oxalis, Mnium undulatum*	5·15	496 *t*	1	1	*Q.* Flush	
			Oakwood (Yorkshire)					
52.	Alne	*Dryopteris filix-mas, Deschampsia caespitosa* a.	4·77	376	3	1		—
53.	,,	*Sanicula, Ranunculus repens* a.	4·80	387	2	1	*Q.* Worms	
54.	,,	*Circaea lutetiana, Deschampsia caespitosa* a.	5·08	529	1	2	*F, Q*	
55.	Tollerton	*Agrostis vulgaris-Oxalis* a.	3·87	544	3	1		—
56.	Ilkley	*Urtica* a., *Dactylis, Agrostis alba*	6·91	483	0	1	Flush	
57.	Pillmoor	*Urtica* a., *Dryopteris dilatata*	4·35	—	3	2	*Q*	
58.	Fosse wood	*Urtica* a.	5·30	528	1	4	Worms	
59.	Grasswood	*Spiraea Ulmaria* a., *Geranium sylvaticum, Geum urbanum*	5·82	512	1	2	Ash-oak	
			General oakwood (Lake District)					
			Teucrium Scorodonia abundant					
60.	Red Nab	*Lychnis dioica, Lonicera*	3·87	455	3	2	*Q*	
61.	,,	*L. dioica, Oxalis*	4·37	480	2	1	*A.* Worms	
62.	Cunsey	*Digitalis, Oxalis*	4·35	465*	3	3	*Pa*	
63.	,,	*Deschampsia flexuosa, Hypnum cupressiforme*	3·98	475 *t*	3	1		—
64.	Wray	*Catharinea undulata, Lychnis*	4·05	422*	3	2	*B.* Worms, little humus	
65.	Bortree	*Oxalis, Hypnum cupressiforme*	4·54	458 *t*	2	1	*Taxus* wood	
66.	,,	*Primula vulgaris, Brachypodium*	5·32	—	1	2	*T.* Above *Taxus* wood	
			Deschampsia flexuosa abundant					
67.	Cunsey	*Galium saxatile* a.	3·92	446 *t*	3	1		—
68.	Bortree	*G. saxatile, Teucrium*	3·85	398	2	1	*B.* Little humus	
69.	Roudsea	*G. saxatile, Oxalis*	3·68	456	3	—		—
			Agrostis vulgaris-Anthoxanthum odoratum abundant					
70.	Red Nab	*Deschampsia flexuosa*	3·97	418	3	2		—
71.	Bella Grange	*Holcus mollis*	4·50	466*	2	2	*A, Q, T*	
72.	Hawkshead	*Deschampsia flexuosa, Galium saxatile*	4·11	527	4	1	*Q.* Worms	

	Place	Ground flora	pH	E_5	Thio-cyanate	Nitrate	Seedlings and Remarks
			Unaltered glacial drifts				
73.	Wray	30 cm. depth	4·85	365	0	2	—
74.	Coniston	30 cm. depth	4·77	383	0	2	—
75.	Oxenfell	3 m. depth	4·91	—	0	—	—
			Dicranum majus				
76.	Wray	*Polytrichum commune*	3·78	404	2	—	—
77.	,,	*Leucobryum glaucum*	3·38	410*	1	—	—
78.	,,	*Hylocomium loreum* a.	3·68	425*	3	—	—
79.	Mary Glen	*H. loreum* a.	3·85	465	4	1	*Q*
80.	Roudsea	*H. loreum* a.	3·53	437 *t*	3	—	—
81.	Red Nab	*Mnium hornum*	3·72	398	3	—	*Pa*
82.	,,	*Polytrichum commune* a.	3·74	345*	2	—	*B*
			Birchwood				
83.	Nor Moss	*Molinia* a.	3·64	407	1	—	—
84.	Out Dubs	*Molinia* a., *Potentilla erecta*	3·44	453*	2	—	*Frangula* present
85.	Ullock	*Molinia*, *Sphagnum* a., *Dryopteris dilatata*	3·50	398	3	—	*Frangula* 35%
86.	,,	*Vaccinium Myrtillus* a., *Dicranum majus*	3·38	448	4	—	
87.	,,	*V. Myrtillus* a., *Hypnum Schreberi*	3·44	418	3	—	
88.	,,	*Dryopteris dilatata* a., *Athyrium filix foemina*	3·34	492	4	—	Pine frequent
89.	,,	*D. dilatata*, *Agrostis alba*, *Viola palustris*	3·80	447	3	1	Ash dying 20%
90.	Roudsea	*D. dilatata* a.	3·29	441 *t*	3	—	—
91.	Pillmoor (Y)	*Molinia* a., *Potentilla erecta*	3·28	—	4	—	Damp heath
92.	Adel Moor (Y)	*Molinia* a., *Vaccinium*, *Myrtillus*	3·59	456 *t*	3	—	230 m.
			Alder Series				
93.	Stable Hills	*Phragmites* d., *Salices*	5·66	25	1/3	—	*Salix decipiens* 33, *S. cinerea* 30, *S. viminalis*, 10, *S. fragilus* 10, *Alnus* 15
94.	,,	*Salices* d., *Phragmites*	6·40	372	1	1	
95.	,,	*Salices* d., *Phalaris*, *Spiraea*	7·14	588	1	3	
96.	,,	*Spiraea*, *Phalaris*, *Urtica*	6·64	414	1	1	*Alnus* 66, *Salix fragilis* 21, Ash 6, Oak
97.	,,	*Spiraea*, *Phalaris*, *Urtica*	6·06	471	1	2	
98.	,,	*Spiraea*. *Phalaris*, *Urtica*	4·40	436	2	1	
99.	,,	*Phalaris*, *Spiraea*, *Athyrium filix foemina*	4·04	440	4	1	*Alnus* 48, *Betula* 32
100.	,,	*A. filix foemina*, *Dryopteris dilatata* f.	4·03	357	3	—	
101.	,,	*Urtica*, *Rubus idaeus* f.	6·56	517	1	3	Ash 70, *Salix fragilis* 16, *Alnus* 8, *Acer* 6
102.	,,	*Urtica*	5·98	504	2	2	
103.	Esthwaite	*Typha latifolia*	5·31	32	1/3	—	Zone of rapid silting
104.	,,	*T. latifolia* (by stream)	5·80	80*	1/4	—	
105.	,,	*Salix decipiens-purpurea* thicket	5·45	355	2	3	Jan. E_5 40
106.	,,	*Alnus*, *Phalaris*, *Urtica*	5·44	422*	2	2	Jan. E_5 298
107.	,,	*Alnus*, *Spiraea*, *Juncus effusus*	5·34	401	4	3	Jan. E_5 260
108.	,,	*Juncus effusus*, *Angelica*, *Holcus lanatus*	4·58	342*	4	1	Oldest part of zone
109.	,,	*J. effusus*, *Angelica*, *Holcus lanatus*	4·82	355	4	2	

Salix cinerea series

110.	Esthwaite	*Phragmites* d.	5·10	70	0/3	—	—
111.	,,	*Phragmites* a., *Typha latifolia*	5·45	90	0/3	—	—
112.	,,	*Carex elata* a., *Iris*	5·12	15*	1/4	—	Young *Salix* plants
113.	,,	*C. paniculata*, *Spiraea* a.	5·08	58*	0/3	—	
114.	,,	*Juncus sylvaticus*, *Hypnum cuspidatum* a.	5·32	70	1/3	—	Young *Salix* wood
115.	,,	*Spiraea*, *Iris* a.	5·16	225	1/2	—	
116.	,,	*Sphagnum*, *Menyanthes* a.	4·76	300*	2/3	—	
117.	,,	*Sphagnum* a., *Lychnis flos-cuculi*, *Juncus sylvaticus*	4·66	312	2/3	—	Centre, *Betula* present
118.	,,	*Sphagnum* a., *Carex elata*, *Viola palustris*	4·87	313*	2/3	—	Oldest, *Betula* 10–25 %
119.	Rusland	*Carices* a., *Menyanthes*, *Lychnis flos-cuculi*	5·22	135	1/4	—	
120.	,,	*Spiraea*, *Climacium dendroides* a.	5·20	183 *t*	2/4	—	*Salix* 95, full grown
121.	,,	*Molinia* a., *Athyrium filix foemina*	5·00	317	3/4	—	
122.	,,	*Molinia* a., *Athyrium filix-foemina*, *Sphagnum*	4·84	352 *t*	3	—	*Salix* 54, *Betula* 26, *Frangula* 20
123.	Brothers Water	*Molinia* a., *Sphagnum*	5·18	342 *t*	2/3	—	
124.	,,	*Molinia* a., *Sphagnum*, *Spiraea*	5·02	365	3	2	Old, *Salix* 67, *Betula* 33
125.	,,	*Juncus sylvaticus*, *Sphagnum* a. opening	5·08	345	2	—	
126.	,,	*Spiraea* a., *Phalaris*, *Climacium* f.	6·72	590	1	2	Ash 25 %, flushed gravel below
127.	Malham T.	*Spiraea*, *Climacium*, *Hypnum cuspidatum* a.	5·76	122	0/1	—	*Salix* developing
128.	,,	*Mnium punctatum* a., *Crepis paludosa*, *Menyanthes*	5·10	203	0/2	—	Thicket
129.	,,	*Sphagnum* d., *Menyanthes*, *Narthecium*	3·82	321	3/4	—	*Salix* dying
130.	Roudsea T.	*Phragmites* d., *Carex acutiformis*	7·07	0 *t*	0/4	—	—
131.	,,	*Iris*, *Phragmites* d., *Carex acutiformis*	6·11	345 *t*	0/1	—	
132.	,,	*Solanum Dulcamara*, *Calamogrostis lanceolata*, *Carex laevigata*	5·09	339 *t*	0/2	—	*Salix* 42, *Alnus* 24, *Betula* 15, *Viburnum* 10

THE SIGNIFICANCE OF PERCENTAGE AREA DETERMINATIONS YIELDED BY THE PERCENTAGE AREA OR DENSITY LIST METHOD OF PASTURE ANALYSIS

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In the percentage area method of pasture analysis the percentage of ground covered by every species in a quadrat is estimated. The method is used to study quantitatively the effects of succession or the changes induced by treatment in grassland.

History of method

Armstrong, who in 1907 introduced the percentage area method, used a square foot quadrat frame subdivided into 144 equal squares. "The percentage of ground occupied in plan by each species was estimated by eye on each square inch" (Davies, 1931). Sampson (1923) and other American workers modified this technique considerably, and adapted the method to prairie and range conditions.

In the density list method, as it is termed in America, a square metre quadrat frame is subdivided into 100 sq. dm. and the percentage area estimations are recorded on a special form which too is subdivided into 100 squares. The percentage area estimated for each species in each square decimetre is listed in the corresponding square on the form. At the Frankenwald Botanical Research Station of the University of the Witwatersrand, the percentage area method has been developed and rendered suitable for the analysis of grass veld in South Africa.

Murray & Glover (1935) describe a greatly improved square metre quadrat and the method in which it is used. "With a frame of this type the detailed botanical analysis of each selected site was made in the following manner. In each decimetre square, estimations were made of the percentage of ground covered by the various species present, and entered in the corresponding square of a blank diagram of the quadrat together with the total percentage cover of all the species occurring in the square. The estimations were all made at ground level, thereby giving the basal cover, and in order to assist in judging this, a small movable frame was used which divided each decimetre square into 25 equal parts so that one of these subdivisions represented 4% of the area. Besides making the entries described, the percentage cover of each species was also entered under the name of that species on a separate sheet so

that the totals could be readily worked out for the whole quadrat. This means making two entries in the field for each estimation." On a further sheet the percentage of the total cover contributed by each species is entered. Thus the percentage area method supplies the following data:

(1) the percentage area of ground covered by vegetation at ground level,
(2) the percentage area of ground that each species covers at ground level, and
(3) the percentage each species contributes to the total basal cover.

West (1937) has pointed out that the percentage contributed by each species to the total basal cover is not related in any way to the percentage herbage contributed by the species to the total yield. When the value and the growth form of the individual species is known, the significance of their percentage basal areas in relation to yield may be gauged to some extent, but this is an indirect and inexact means of arriving at the value of the individual contribution of any species to the herbage.

Hall & Murray (1935), comparing percentage area productivity methods, showed that in veld where the yield had been considerably increased by means of proper veld management and fertilizing, the improvement clearly demonstrated by the percentage productivity method was not shown by the percentage *area* method. The percentage area method gives no information as to yield, nor does it supply any information as to the importance, in terms of forage, of the constituent species. These are the chief objections to the percentage area method. On the other hand the method presents many advantages. It gives a very good picture of the structure of the vegetation, and for this reason is of great value in the study of the ecology of grassveld and pasture. When permanent percentage area quadrats are laid down the increase or decrease in importance of the individual species due to succession or different treatments is easily followed, and invasion by weeds or other indications of incorrect management can be detected and studied. The percentage area of ground covered is in itself a very useful result and important in arriving at a quantitative idea of the veld under consideration. As a definite value it is useful in the description and comparison of different types of veld. The data yielded by this method are very suitable for statistical analysis, and although the percentage area results are not a sensitive measure of change in yield, they definitely reflect any change in the nature of the plant cover. The method is tedious, but all exact methods of analysis exhibit this disadvantage, and area for area on the same quadrat less time is spent on a percentage area determination than is needed for charting by any other method. It has been shown too (West, 1937) that the square metre quadrat size is unnecessarily large and that on the Frankenwald "Purple Veld"[1] a 25 sq. m. quadrat is the most convenient size, combining economy of time and labour with accuracy.

[1] So-called on account of its general tint in the dry season.

The problem

If the percentage area method of pasture analysis is used to study change in grassland, it is necessary to be able to tell when a difference in the percentage area determinations indicates that a change has taken place in the pasture analysed. The percentage area method is subjective, the results on any quadrat being obtained by personal estimation. It is recognized that different observers estimate differently and, in order to obtain comparable results, this difficulty introduced by the personal factor has been attacked from two different angles. The existence of the personal factor error is recognized, and in the hope that this remains constant for any one observer an endeavour is made to have quadrats re-listed by the original lister. On the other hand, attempts have been made to eliminate as far as possible, the personal factor error by making the method of determination an objective one. The listing square as used by Murray & Glover (1935) is a step in this direction, but it does not go far enough. Even when a listing square is continually employed, personal judgement must still be exercised and the method is still a subjective one. Mechanical charting by pantograph is a much greater advance in the direction of a totally objective method, but due to limitations imposed by time and labour this does not solve the difficulty.

The investigation

In order to investigate the accuracy of the percentage area method the following trials were made:

Trial A. A square metre quadrat laid down in typical "Frankenwald Purple Veld" was listed by three different observers during the months May and June 1936. The observers were well acquainted with the method and each had had considerable experience in making percentage basal area determinations. A listing square was not used, but otherwise the quadrat was listed in the usual manner. Separate determinations were made for each species within each square decimetre subdivision. The plants found on this quadrat, listed in order of the area occupied, were:

Digitaria tricholaenoides Stapf.
Tristachya hispida (Thunb.) K. Schum.
Trachypogon plumosus Nees.
Elionurus argenteus Nees.
Schizachyrium semiberbe Nees.
Digitaria monodactyla Stapf.
Eragrostis chalcantha Trin.
Monocymbium ceresiiforme Stapf.
Helichrysum sp.
Diplachne biflora Hack.
Themeda triandra Forsk.
Alloteropsis semialata Hitchcock
Sporobolus sp.
Andropogon amplectens Nees.
Brachiaria serrata Stapf.
Euryops sp.
Michrochloa caffra Nees.
Heteropogon contortus R. & S.
Oldenlandia sp.
Eragrostis brizoides Nees.
Becium obovatum N.E. Br. var. hians N.E. Br.
Scylla sp.
Thesium sp.
Senecio Serra Sond.
Panicum natalense Hochst.

The quadrat was listed four times with the following results:

Table I

Mean percentage area covered as determined by different observers on the same 100 sq. dm. quadrat.

Observer	Date	Mean percentage area covered
R. Story (A)	10. v. 36	18·29
O. West	16. v. 36	17·69
R. Story (B)	25. v. 36	15·35
P. Glover	18. vi. 36	20·41

The veld was quite dormant during the period 10 May to 15 June, and if, as is probable, the wear and tear occasioned by the identification of species and the estimation of the area they occupied caused some lessening of the cover on the quadrat, this is not reflected in the results obtained; the last value obtained by P. Glover being higher than any of the previous estimations.

Using the correlation formula $R_{xy}=\dfrac{\Sigma xy-N.\bar{x}.\bar{y}}{\sqrt{(\Sigma x^2-N\bar{x}^2)(\Sigma y^2-N\bar{y}^2)}}$, the estimations made by the different observers were correlated. The figures used in obtaining the correlation coefficients were the percentage area covered determinations for each of the 100 sq. dm. of the quadrat. The correlation coefficients obtained, together with their probable error, are given in Table II.

$$\text{P.E.}=0{\cdot}6745\left(\frac{1-r^2}{\sqrt{N}}\right).$$

Table II

	R	P.E.
Story A with Story B	0·761	0·028
Story A with West	0·774	0·027
Story A with Glover	0·848	0·019
Story B with West	0·788	0·026
Story B with Glover	0·720	0·032

It is obvious that in all cases the correlation is very high.

Trial B. During the period, 22 August to 6 September 1936, 20 sq. dm. located in camp Little Q. 1 were listed several times by West, Rose-Innes and Glover both with and without the listing square. The percentage of the area covered on each square decimetre was determined. No attention was paid to species. The determinations made are tabulated below (see Table III).

These determinations were then correlated. The results are shown in Table IV.

The correlation in all cases is very high, but curiously enough the correlation obtained when the listing square was used is not higher than that obtained without it. It must be remembered, however, that all the observers had had considerable practice in the method and, as is apparent, estimated as consistently with and without the aid of the listing square.

Table III

Estimations made with the aid of the listing square				Estimations made without the aid of the listing square				
West		Glover	Rose-Innes	West		Glover		Rose-Innes
A	B	A	A	C	D	B	C	B
17	14	20	17	17	15	20	15	17
12	12	8	11	8	11	10	10	13
2	1	2	1	1	2	2	1	2
6	8	8	9	7	6	10	8	11
6	7	4	5	5	5	8	6	7
12	14	10	10	7	9	12	12	13
28	36	36	36	30	25	35	30	15
20	22	20	12	12	12	20	15	13
8	11	10	10	8	6	11	12	11
1	2	1	1	2	1	3	3	3
12	14	16	14	12	10	16	12	14
10	8	9	10	6	6	8	7	10
4	3	4	3	3	6	3	4	2
13	16	20	15	9	9	15	10	14
14	19	36	14	14	16	25	15	16
50	58	56	60	55	50	60	60	40
6	8	8	5	4	7	8	8	8
1	1	2	2	2	1	2	2	3
12	12	9	4	10	10	10	7	7
60	55	48	36	55	53	50	50	47
294	**321**	**327**	**275**	**267**	**260**	**328**	**287**	**266**
14·7	16·05	16·35	13·75	13·35	13·0	16·4	14·35	13·3

Table IV

	R	P.E.
West with listing square (A and B)	0·980	0·006
West without listing square (C and D)	0·985	0·005
West with and without listing square (A and C)	0·987	0·004
West and Innes with listing square (A and A)	0·898	0·029
West and Innes without listing square (A and B)	0·950	0·015
Innes with and without listing square (A and B)	0·870	0·037
West and Glover with listing square (A and A)	0·833	0·046
West and Glover without listing square (C and B)	0·977	0·007
Glover without listing square (B and C)	0·976	0·007
Glover with and without listing square (A and B)	0·978	0·007

Practical difficulties

During the course of the work various practical difficulties arose. It was found that the process of listing denuded the quadrat. This limited the number of observations that could be made. Secondly, it was found that once an observer had listed a quadrat he remembered the estimations made. Because of this, as long an interval as possible was allowed to elapse between listings made by the same observer.

Discussion

The correlation obtained shows a definite relation between the measurements obtained by different observers, but such results are not comparable until they have been reduced to the same scale. When the correlation coefficient for the results obtained by two different observers is known, it

is possible to compute by means of a regression equation what one of the observers would measure from what the other observer has measured. For example in the 100 sq. dm. quadrat the correlation coefficient for Story B and West is 0·788. Using the formula

$$Y = R\frac{\sigma_y}{\sigma_x}x - R\frac{\sigma_y}{\sigma_x}\bar{x} + \bar{y}$$

where x = Story B, y = West, Y = the estimated value for West from the known value of Story B,

$$\sigma_y = \sqrt{\frac{\Sigma y^2}{N} - \bar{y}^2},$$

$$\bar{x} = 15{\cdot}35,$$

$$\bar{y} = 17{\cdot}69,$$

$$\sigma_x = \sqrt{386{\cdot}25 - (15{\cdot}35)^2} = 12{\cdot}3,$$

$$\sigma_y = \sqrt{493{\cdot}41 - (17{\cdot}69)^2} = 13{\cdot}4,$$

$$R_{xy} = 0{\cdot}79,$$

$$\frac{\sigma_y}{\sigma_x} = 1{\cdot}089,$$

$$R\frac{\sigma_y}{\sigma_x} = 0{\cdot}8606,$$

$$R\frac{\sigma_y}{\sigma_x}\bar{x} = 13{\cdot}15,$$

$$Y = 0{\cdot}861x + 4{\cdot}54.$$[1]

In deciding the significance of change in percentage area results obtained by different observers, it is necessary to reduce all observations to the scale of one observer. Thus quadrats done by Smith in 1921 and redone by Brown in 1924 must be reduced to one observer's scale, and this can only be done if a correlation can be obtained for the measurements made by Smith and Brown. In order to obtain this correlation, it is necessary that Smith and Brown should list identical quadrats at more or less the same time and that the correlation coefficient should be worked out from their results. Then, presupposing that Smith's and Brown's scales remain constant through the years, it would be possible to compare the results obtained by Smith in 1921 with those obtained by Brown in 1924. In practice, however, it is highly improbable

[1] P.E. of estimation of $Y = 0{\cdot}6745\ \sigma_y\sqrt{1-R^2}$
$= 0{\cdot}6745\ \sigma_y\sqrt{1-0{\cdot}624}$
$= 0{\cdot}6745 \times 13{\cdot}4 \times 0{\cdot}376$
$= \pm 3{\cdot}398.$

West = 0·861 Story B + 4·54 with a probable error of ±3·398.

that any observer's scale of estimation would remain constant from year to year. In order to circumvent this and other obvious difficulties, it is suggested that every observer's estimations be correlated with the measurements obtained by means of the pantograph (Pearse *et al.* 1935). The measurements obtained by means of this instrument are accurate and entirely objective, and would afford a much needed constant scale to which the estimations made by different observers could be reduced. An observer would estimate a number of quadrats in the ordinary manner. He would then determine the percentage basal area on these same quadrats by means of the pantograph and correlate the two sets of results.

The necessary correlation having been obtained, he would use it to reduce all percentage area estimations made by him to the pantograph scale. At regular intervals he would check his correlation coefficient by estimating and then pantographing a number of quadrats. This would make all percentage area estimations directly comparable, and this comparison would not be affected by the interval between the listing and re-listing of quadrats or by the different personal factors introduced by different observers.

Summary

The percentage area method is described and discussed. The difficulty of using estimated percentage area results for the detection of change in pasture or grassland is pointed out.

It is shown that although a strong correlation exists between the estimations made by different observers on the same quadrat, each observer estimates differently and that the results of several observers cannot be compared until such have been reduced to the same scale.

It is proposed that the measurements of area covered made by means of a pantograph be used as a constant scale, that all observers correlate their estimations with pantograph measurements at regular intervals and that they reduce all estimated percentage area results to the pantograph scale. This would make all percentage area results directly comparable, and this comparison would not be affected by the interval between the listing and re-listing of quadrats or by the different personal factor introduced by different observers.

It is concluded that, in deciding on the significance of change shown in results obtained by different observers at different times, it is necessary

(1) to reduce all observations to the same scale;

(2) to compute the standard deviation of the difference of the means and to compare the difference with its standard deviation, or with the derived value, the probable error.

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A CHALK FLORA ON THE LOWER GREENSAND: ITS USE IN INTERPRETING THE CALCICOLE HABIT

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(*With Plate I*)

I. INTRODUCTION

Since progress in plant ecology suffers from the small proportion of experimental as compared with descriptive and observational work, any ecological experiments which are accidentally performed (e.g. Summerhayes & Turrill, 1927) are valuable, although they may lack precision and leave much to be desired when compared with an experiment designed for a particular purpose.

In the following pages a description is given of a small piece of grassland, on soil which provides the accidental experiment through having been made chemically like that of the chalk, while it is physically typical of the greensand. Comparison of the flora of this area with the chalk and greensand floras enables certain conclusions to be drawn as to the relative influence of chemical and physical soil factors in determining the calcicole and calcifuge habits of some of the species. Doubtless more widely collected data will show some amendments to be necessary; but quite apart from the conclusions drawn here, it may be useful in future studies to have a record of the plants in this particular place and of the conditions under which they occur.

Definitions

(1) The factors controlling the occurrence of species in relation to calcareous and acid soils are complex (Salisbury, 1920), and the terminology relating to the subject is confused and inexact. The present paper seems hardly the place to attempt to deal thoroughly with the problem of terminology. It is necessary, however, to explain at once what is meant here by the terms "calcicole" and "calcifuge".

They are used in this paper in what is perhaps their most usual sense. *Calcicoles are regarded as species affecting the more important types of calcareous soils and rare on or absent from acid soils, and calcifuges as the reverse.*

Etymologically this use of the words is far from ideal, particularly as they do not provide for as full a contrast as that of the definition; but the alternative possibilities have equal or greater drawbacks for the present purpose.

(2) It must be remembered that seemingly dogmatic statements about the behaviour of species in regard to soil express only the general preference, and

that *included in such statements are all apparent preferences which are really due to the effects of competition.* The growth of isolated specimens of a given species may show identical vigour on the chalk and the greensand, yet its occurrence on these two soils in the natural vegetation may differ widely owing to the different sets of species with which it has to compete, or to the presence of a handicap on one of the soils which is only manifested in competition. The class of calcifuges, for instance, would include relatively few species if the word were used only for those which, free of all competition, could not grow on calcareous soil, and it is more valuable to employ the word for species whose powers of competition are so reduced by calcareous soil that they do not occur there in ordinary closed vegetation or the limited amount of bare soil associated with it. The failure to separate competition effects from direct soil effects is recognized as a serious shortcoming, but owing to the impossibility of distinguishing between them without protracted culture experiments, this desirable refinement must be omitted for the present.

(3) The expression "chemically (or physically) determined calcicole (or calcifuge)" is frequently used in the following pages. To illustrate the use of the expression: a physically determined calcifuge is a species more or less unaffected by the chemical differences between calcareous and acid soils, found on the latter but not the former by virtue of the physical properties which distinguish them.

(4) It is impossible in the present paper to enter into a full discussion of the distribution of the species concerned on all types of calcareous and acid soils. *The calcicole or calcifuge nature (as defined above) of the species are therefore considered in this work only in relation to the chalk and the greensand floras, under dry conditions.*

In view of the widespread occurrence of these two types of vegetation in the Weald district of England, and of the striking contrast in character which they offer, it may be useful to analyse the causes of some of the floristic differences.

II. DESCRIPTIVE

The vegetation being considered consists of a piece of rough grassland occupying a small and rather sharply bounded area of about 0·75 hectare (2 acres) on the Folkestone beds of the Lower Greensand, not far from Abinger in Surrey. The area is within 1 km. of the chalk escarpment of the North Downs.

This small region will be called the "calcareous sand". The soil is an ordinary sand in texture, but is rendered markedly calcareous by the admixture of chalk in a fairly uniform manner over the area. For the most part the area slopes gently towards the south. It is roughly square, bounded by woods on two sides and by a road on a third. The margins are being very slowly invaded by shrubs and young trees, and a few of these are dotted about on one end of

the area itself. The surrounding woody plants are a typical greensand collection except that there is an unusual abundance of *Euonymus europaeus*, and one specimen of *Clematis vitalba*. The grassland is subject to moderate rabbit attack.

Attention was confined to the herbaceous vegetation, outside the influence of the scrub and woodland. The greater part of it is somewhat disturbed grassland with associated bracken (Phot. 1). At a first glance the grassland strikes one as differing in no important respects, as regards floristic composition, from many typical grasslands of the chalk downs. It was this striking similarity which first drew my attention to the area.

The local occurrence of unexpected species in a region, consequent upon the artificial creation of small habitats of different character, is often observed—for example the calcicolous plants occurring locally where lime had been dropped beside a quarry railway in a mainly siliceous region in Derbyshire (Watson, 1918).

The grassland is composed of three parts:

(1) Grassland proper (with *Pteridium*).
(2) Half-bare ground being colonized.
(3) Trampled pathways covered with short turf.

(1) *The grassland proper*

Over the major part of the grassland *Pteridium aquilinum* is present as a sparse upper layer, but in most places it probably has very little effect on the other herbaceous vegetation. Its average height is about 50 cm. (varying from 30 to 70 cm.), and it is yellowish green in colour ("lime chlorosis"). The real dominant of the grassland proper is not *Pteridium* but *Bromus erectus*, which forms a layer 6–8 cm. high. Other herbs are conspicuous locally. The total list, which purports to be complete for flowering plants, is given in Table I (p. 222). Other data in this table are explained later.

(2) *Half-bare ground being colonized*

This habitat was created three or four years before the plants were listed, by the removal of the turf for use along a roadside. The vegetation is now very mixed and has no single species playing a leading rôle. Nearly all the species of the grassland proper are also found on the half-bare ground, including *Pteridium*, which occurs sparsely. In addition to these are some species not found in the grassland proper (given in Table II, p. 224).

(3) *Trampled pathways*

The paths bear a heterogeneous covering 0·5–1 cm. thick. *Pteridium* is of course absent. Here and there a mixture of moss species is locally dominant. The chief species of the grassland proper also occurring on the paths are:

Phot. 1. Part of the calcareous sand area. Grassland dominated by *Bromus erectus* in the foreground. One of the trampled pathways on the left. Sparsely growing *Pteridium* in middle distance. The ruler is 30 cm. (1 ft.) high and is standing immediately against a *Pteridium* frond.

Phot. 2. Part of the acid sand area. *Agrostis tenuis* turf. Outlying *Pteridium* fronds in centre, thick masses of it on right and in background.

Festuca rubra	l.d.	Plantago lanceolata	l.a.
Hieracium pilosella	a.	Bromus erectus	l.f.
Koeleria gracilis	l.a.		

Also there are on the paths some species not found in the grassland proper (see Table II).

HISTORY

A forester living in the neighbourhood has informed me that the calcareous sand area has been in its present state as long as can be remembered by anyone in the immediate locality, that is to say for 50 years at the least.

The most probable explanation of the chalk and flints which are scattered in the soil is that they were spread over the area at some time when it was cultivated, and in this case ploughing would account for the uniform distribution of chalk in the soil. There is a disused lime kiln about 90 m. (100 yd.) from the area, and most likely the small flints were deposited with the waste chalk from this kiln. The probability of cultivation at some past date is enhanced by the fact that the area is square and surrounded by low banks.

There will have been at least one important result upon the present calcicolous flora if the area was once arable. When cultivation ceased and the ground was left to colonizing plants, any calcicoles from the neighbouring downs would have a fair chance of invading the open or immature community of weeds which must at first have existed, and therefore they would have become established relatively quickly. If, on the other hand, the area had never been bared by ploughing, invasion of a closed community by calcicoles, following the scattering of chalk, would have been much slower. Chalk has in the past been transported in quantity from the downs to the neighbouring lime kiln and this has no doubt assisted the arrival of species from the downs.

Because of these considerations and the fact that the vegetation has been of the same general nature for at least 50 years, it is permissible to make an analysis of the flora on the assumption that the grassland proper now contains virtually its final complement of species under the present biotic and edaphic conditions. Cases where this assumption is not warranted are specified in the subsequent discussion.

ACID SAND AREA EXAMINED FOR COMPARISON

The vegetation and soil of the calcareous sand area were compared with those of an area of similar character about 230 m. (250 yd.) away, also on the Folkestone beds but without chalk in the soil and therefore of the acid type characteristic of these beds (Phot. 2). This latter area is about the same size as that of calcareous sand, like it bearing a vegetation of grassland and bracken and similarly affected by rabbits. It is however flat, not sloping, and is much less frequented by people. In general character it affords a good parallel with the calcareous sand area, and has therefore been taken as giving a rough representation of the flora which would have existed in the calcareous area if chalk had not been added to it.

The grassland consists of turf 2–6 cm. thick, surrounded by *Pteridium*, which, in contrast to that of the calcareous sand, grows very thickly where it grows at all, is of average height 90 cm. (varying from 30 cm. to 1·8 m.), and is of the typical rich green colour in summer. The subsidiary flora of the *Pteridium* zone was not considered, as it is in no way parallel to that studied on the calcareous sand.

Habitats comparable with (2) and (3) of the calcareous sand are poorly represented. There is a little bared ground round a small rabbit warren, and one pathway, which however is not used nearly as much as those on the calcareous sand. The area is also farther from agricultural land, so that the influx of seed due to these two human influences is probably less.

Table I. *Flora of the calcareous sand (grassland proper) and of the acid sand area*

(1) *On calcareous sand only* (41 spp.).

	Frequency	Constancy in chalk grassland[1]		Frequency	Constancy in chalk grassland
Dominant or abundant:					
Bromus erectus	d.-sd.	4	Thymus serpyllum	a.	5
Lotus corniculatus	a.	5	Helianthemum vulgare	f.-l.d.	—
Frequent, occasional or local:					
Medicago lupulina	f.	3	Scabiosa columbaria	o.	5
Cirsium acaule	l.f.	5	Arenaria serpyllifolia	l.	—
Sieglingia decumbens	l.f.	—	Carlina vulgaris[2]	l.	3
Poterium sanguisorba	o.-l.a.	5	Lathyrus pratensis	l.	—
Agrostis alba	o.	3	Poa pratensis	l.	—
Avena pubescens	o.	4	Linum catharticum	r.-l.a.	5
Briza media	o.	5	Carex flacca	r.-f.	5
Holcus lanatus	o.	3	Saxifraga granulata	r.-l.f.	—
Ranunculus bulbosus	o.	4			
Rare:					
Arrhenatherum elatius		—	Pimpinella saxifraga		5
Centaurea nemoralis		4	Polygala vulgaris		3
Dactylis glomerata		4	Potentilla reptans		—
Epilobium montanum		—	Sagina apetala		—
Fragaria vesca		—	Scabiosa arvensis		—
Galium mollugo		3	Trifolium arvense		—
Hypericum perforatum		—	T. pratense		5
Leontodon hispidus		5	T. procumbens		—
Myosotis arvensis		—	T. scabrum		—
Ononis repens		—	Trisetum flavescens		4

(2) *More abundant on calcareous sand* (12 spp.).

	Calcareous sand	Acid sand	Constancy in chalk grassland
Pteridium aquilinum	v.a.,l.d.	l.d.	—
Festuca ovina	a.	o.,l.cd.	5
F. rubra[3]	a.	l.f.	5
Carex caryophyllea	a.	l.	3
Galium verum	a.	o.	4
Hieracium pilosella[4]	a.	l.a.	4
Koeleria gracilis	a.	r.	5
Veronica chamaedrys	l.f.	r.	3
Plantago lanceolata[4]	o.-f.	l.	5
Achillea millefolium[5]	o.-l.f.	l.f.	4
Cerastium vulgatum	o.	r.	3
Hypochaeris radicata	o.	r.	—

Table I (*cont.*)

(3) *Equally abundant on both* (2 spp.).	Calcareous sand	Acid sand	Constancy in chalk grassland
Leontodon autumnalis	r.	r.	—
Senecio jacobaea	r.	l.	—
(4) *More abundant on acid sand* (5 spp.).			
Luzula campestris	f.-a.	a.	—
Campanula rotundifolia	o.	a.	4
Rumex acetosa	o.	a.	3
Agrostis tenuis[6]	r.-l.d.	d.	·
Rumex acetosella	r.	a.	—

(5) *On acid sand only* (15 spp.), constancy in chalk grassland below 3.

Anthoxanthum odoratum	a.	Veronica officinalis[5]	l.
Calluna vulgaris[7]	l.	Aira praecox	r.
Deschampsia flexuosa[8]	l.sd.	Myosotis collina	r.
Stellaria graminea	f.	Potentilla sterilis	r.
Galium saxatile	l.f.	Taraxacum erythrospermum[4]	r.
Holcus mollis[5]	l.f.	Trifolium filiforme	r.
Myosotis versicolor[5]	l.f.	Vicia angustifolia	r.
Ornithopus perpusillus	o.,l.a.		

Bryophytes and lichens[9]

On calcareous sand only.

Hylocomium splendens	r.,l.a.	Camptothecium lutescens	r.
Weisia sp. (microstoma or viridula)	l.	Hypnum cupressiforme	r.
		Cladonia silvatica	l.f.
Brachythecium rutabulum	r.	C. fimbriata	l.
Bryum inclinatum	r.	Peltigera rufescens	r.

On both areas

	Calcareous sand	Acid sand
Brachythecium purum	a.	v.a.
Dicranum scoparium	l.v.a.	r.
Polytrichum juniperinum	r.	l.a.

On acid sand only.

Hylocomium squarrosum	l.a.
Bryum caespiticium	o.
Mnium affine	r.

Notes to Table I

Symbols employed: d. = dominant, sd. = subdominant, cd. = codominant, a. = abundant, f. = frequent, o. = occasional, r. = rare, l. = local(ly), v. = very.

[1] Constancy. 3, 4, 5 are constancy figures for the occurrence of these species in chalk grassland, taken from Tansley & Adamson (1926). Reference may be made to their paper for the basis on which these figures are given. Species of constancy 1 and 2 are not marked, as they are of no particular significance for the present purpose.

[2] *Carlina vulgaris* here grows much taller and with more capitula to a plant than it does in chalk grassland. It shows a similar habit on various non-chalk soils.

[3] *Festuca rubra.* Constancy is given by Tansley & Adamson as 2, but further work on chalk grassland has made it clear that there are actually very few sites from which *F. rubra* is absent.

[4] *Hieracium pilosella, Plantago lanceolata* and *Taraxacum erythrospermum* on the acid sand occur only on the trampled pathway.

[5] *Achillea millefolium, Holcus mollis, Myosotis versicolor* and *Veronica officinalis* on the acid sand occur only by the rabbit warren.

[6] The soil round the roots of *Agrostis tenuis* in the turf on the calcareous sand was tested with dilute hydrochloric acid, and gave no effervescence. That round *A. tenuis* clumps colonizing bare ground was also tested and showed a moderate effervescence. On this rather scanty evidence it looks as though *A. tenuis* is here able to tolerate free calcium carbonate when growing isolated, but not in competition with the regular calcicoles of the turf.

[7] Very little *Calluna*. Grazed down.

[8] *Deschampsia flexuosa.* Only close to *Pteridium.*

[9] Bryophytes and Lichens. The commoner of these are listed to make a more complete picture of the communities concerned; but further consideration in this paper would be unprofitable on account of the special difficulties in their ecology.

The species of the disturbed and trampled ground on the acid sand are ncluded in Table I, reference being made to their special habitat in footnotes. This procedure is different from that adopted for the calcareous sand list; it is followed on purpose because there are doubtless a good many species *in the grassland proper* of the calcareous sand owing their presence to the proximity of the extensive disturbed and trampled ground, and the 7 extra species of these habitats on the acid sand serve as a rough equivalent.

Table II. *Calcareous sand area; species restricted to half-bare ground and pathways, number, excluding bryophytes, 23. This list is not exhaustive, but includes all the important species*

	Bare ground	Pathways
Anagallis arvensis	o.	—
Bellis perennis	f.-l.a.	—
Calamintha acinos	r.	—
Capsella bursa-pastoris	—	l.
Cirsium arvense	r.	—
Erodium cicutarium	o.	o.
Erophila vulgaris	a.	o.,l.f.
Erythraea centaurium	f.	f.
Euphrasia nemorosa	r.	—
Melandrium album	r.	—
Myosotis collina	f.-l.a.	r.
Plantago coronopus	l.	a.-cd.
Plantago major	—	l.
Poa annua	—	l.a.
Potentilla argentea	r.	—
Ranunculus acris	r.	—
Sagina nodosa	r.	—
Saxifraga tridactylites	l.f.	—
Sherardia arvensis	l.f.	—
Sonchus asper	r.	—
Taraxacum erythrospermum	o.	—
Thrincia hirta	r.	—
Verbascum thapsus	r.	—
Bryophytes		
Barbula convoluta	a.	—
Ceratodon purpureus	a.	—

III. SOIL

The soil of the calcareous sand area is a sand of dark grey colour. At a depth of 42 cm. it is paler grey. There is no suggestion of the red-brown coloration general in the lower horizon of soils on the Folkestone beds. Nearly everywhere free carbonate was intimately mixed with the soil. Dilute hydrochloric acid produced quite strong effervescence close to the surface and moderate effervescence at 42 cm. The soil was, however, rather variable from place to place. On the highest ground it contained very small chalk lumps, rather small flints, and many pieces of ferruginous sandstone. Occasional patches were encountered, a few square centimetres in extent, which gave no effervescence with dilute acid.

Table A compares the soil of the calcareous and acid areas. The samples for analysis were taken from 8 cm. depth, where there was the greatest intensity

of root development. In each case 7 samples of the same size were taken from different parts of the area (grassland proper, not bared nor trampled ground) and mixed, the analysis being performed on part of this mixture.

Table A. *Comparison of soils*

	Calcareous sand	Acid sand	Typical chalk grassland soil
Profile	Variable. 0–42 cm. grades from dark to pale grey. Ferruginous sandstone lumps, small flints and small chalk lumps occur near surface locally	Uniform. 0–8 cm. light grey grading to brown. 8–40 cm. brown grading to red-brown sand. Ferruginous sandstone lumps occasional	Dark brown crumbly layer with small chalk lumps and a few flints from about 0–12 cm., redder brown and becoming slightly clayey from 12 to 26 cm. with big chalk lumps; grading through buff-coloured material and still larger lumps to fissured rock at *c.* 35 cm.
*p*H	7·4	4·9	7·3
Mechanical analysis:			
Coarse sand	62·4 } 91·6	73·2 } 92·1	41 } 74
Fine sand	29·2	18·9	33
Silt	6·9	6·3	14
Clay	1·5	1·6	12
Air-dry moisture	1·4	0·6	6·3
Loss on ignition	5·0	2·8	23·5
Calcium carbonate	4·5	0·0	36·1
Carbon	2·8	1·4	11·4
Nitrogen	0·22	0·12	1·0
Morgan's colorimetric tests:			
Nitrate	Medium (10)	Low (5)	Low (3)
Ammonia	Medium (12)	Medium high (25)	Low (6)
Phosphate	Medium (25)	Low (10)	Very low (8)
Potassium	Very low (<75)	None	Very low (38)
Calcium	High (1500)	Extremely low but appreciable (<200)	Extremely high (>2000)
Magnesium	Medium (25)	Low (12)	Medium (32)
Aluminium	None	High (125)	None
Manganese	Trace	Medium (12)	Very low (2)
Ferric iron	None	Medium (25)	Trace
Ferrous iron	None	None	None

For comparison the corresponding values for chalk grassland soil are given. They are obtained by the same analytical methods, and are the means of the results for 6 typical chalk grasslands. The Morgan tests on the chalk grassland soil were not done at the same time as those on the two sands, and are therefore not strictly comparable. The Sudan method was used for mechanical analysis. The results for chalk grassland in this item are from samples different from those used in the remaining analyses. The results for these samples are only very approximate because the crumbs did not disperse properly. The coarse sand fraction in the last column contains much that really belongs to the silt and clay.

Carbon (in humus) was estimated by Walkley and Black's method of oxidation with potassium dichromate and concentrated sulphuric acid. The

analytical data are given as percentages of the dry soil, except for the results obtained by Morgan's tests (Morgan, 1935). The figures given there are roughly parts per million, calculated from Morgan's standards, which are based on the results given by ordinary agricultural soils. The tests only indicate the amounts of these ions in the replaceable state, not the total amounts present. The word "none" merely indicates not detectable by this method. The values for ammonia and nitrate, obtained after the samples had been stored for some time, are of doubtful significance.

The differences shown in Table A have some pedological interest quite apart from their bearing upon the vegetation. They illustrate clearly the secondary effects of free chalk upon a sandy soil when compared with one which may be taken to represent the original state before addition of chalk; and it may be noted that these data apply to an uncultivated soil bearing natural vegetation. Although no unknown facts are brought to light regarding the secondary effects of calcium carbonate, it is worth while to list the chief differences:

The calcareous sand is appreciably higher in:

*p*H	Replaceable nitrate
Air-dry moisture	phosphate
Loss on ignition	potassium
Calcium carbonate	calcium
Carbon (humus)	magnesium
Nitrogen	

The acid sand is higher in:

Replaceable ammonia
aluminium
manganese
ferric iron

Probably all these differences are to be regarded as related to the change in *p*H and calcium carbonate content, with the possible exception of the greater amounts of phosphate, potassium and magnesium, one or more of which may have been added as part of the chalk.

IV. COMPARISONS AND DISCUSSION

Now while these two soils differ strikingly from each other in chemical respects, it is obvious that they are far more closely allied to each other in physical properties than either is to a chalk grassland soil—including under physical properties not only the proportions of different sized particles, but also the quantity of humus and therefore (since it is largely controlled by clay and humus) the water-holding capacity. On the other hand the flora of the calcareous sand, as is more fully explained later, shows a great deal in common with chalk grassland and very little in common with that of the acid sand.

The obvious inference is that the flora of chalk grassland is, within a certain degree of soil moisture, determined in the main by the chemical rather than the physical peculiarities of the soil. This conclusion regarding the calcicolous habit is not new (e.g. Crépin, 1864; Watson, 1918, p. 192, regarding bryophytes and lichens), although it has been disputed by Kraus (1911). In the present investigation the soil analysis shows that other chemical differences exist between the calcareous and the acid sands besides *p*H and exchangeable calcium; but there can be little doubt that one or both of the latter are the important chemical agency in the case of the bulk of the flora.

The study of this calcareous sand area does not, however, merely substantiate a view that is now commonly accepted. It is not to be expected that each one of the more particular chalk or greensand species is encouraged by the same factor in the soil which favours it, and the presence of this calcareous sand habitat provides a way (admittedly inexact) of partially sifting the chalk and the greensand floras into categories according to whether their calcicole or calcifuge habit is determined primarily by chemical or by physical soil factors. The need of treating the calcicole flora in this way has been dealt with by Salisbury (1920).

In the following floristic comparisons almost no attention is paid to differences in abundance of species held in common by the regions compared; unwarranted conclusions would be particularly likely if this were done rather than considering presence and absence only, although doubtless there are cases where a big difference in abundance betokens more than the mere absence in one area of a species which is rare in the other.

COMPARISON WITH CHALK FLORA

It will be noticed in Table I that 12 chalk grassland species of constancy 3 or higher[1] are common to the calcareous and to the acid sand and so are simply species of dry grassland regardless of basic or acidic conditions. 23 of similar constancy are found only on the calcareous sand, and if the acid area were regarded as a perfect "control" these would be chemically determined calcicoles. For the mass of the species this approximation is sound, but the "control" is not perfect, as instanced by the presence in this class of *Sieglingia decumbens*, a typical calcifuge.

It is possible to correct for this imperfection—notably the lack of a parallel to the calcareous disturbed areas—by considering records for the entire Lower Greensand flora of Surrey (Brewer,[2] 1863; Dunn, 1893; Salmon, 1931).

[1] This criterion is used only as a guide to indicate the more common chalk grassland plants, and not as having any precise quantitative significance.

[2] Brewer gives a tabulated record showing the occurrence or absence on the Lower Greensand of all the species in his *Flora*. The newer *Flora of Surrey* by Salmon contains references to a good many occurrences not given by Brewer, but the modern *Flora* does not contain a table of species showing their occurrence on soils of the various geological origins. Brewer's *Flora* may certainly be taken as accurate enough regarding important occurrences, and it is these with which we are here concerned, not very rare or isolated occurrences on the greensand or the chalk.

These records include all types of community on all the Lower Greensand beds, and therefore over-compensate for the deficiencies of the acid sand area. Thus, while the acid sand is not an adequate "control" and admits as chemically determined calcicoles certain species which should not be included, the total Lower Greensand records clearly cut out species which should be included; but they do establish beyond doubt that, as a bare minimum, those species occurring nowhere on the Lower Greensand except on the calcareous sand area are present there on account of the chemical peculiarities of the soil.

Species on the calcareous sand and the chalk, not on the greensand

Listing, therefore, only the vascular species from the calcareous sand (all three types of habitat) which are not recorded at all from the Lower Greensand of Surrey, we are left with those in Table III.

Table III

Avena pubescens	Leontodon hispidus
Bromus erectus	Poterium sanguisorba
Helianthemum vulgare[1]	Scabiosa columbaria

All these species are also abundant in chalk grassland, so we can safely regard them as not particular about the physical soil conditions, as between the chalk and the greensand.

It will be observed that *Bromus erectus* falls into the class of chemically determined calcicoles. Yet Braun-Blanquet (1932) states that although it is considered a calcicole in central Europe, it occurs on various types of soil in south Europe, including non-calcareous ones. It is quite possible that *B. erectus* may in all cases prefer calcareous soils, though it may not be dependent on them under the conditions of competition obtaining in south Europe. Also the possibility of separate physiological races must not be forgotten.

Species on the chalk, not on the calcareous sand nor the greensand

Among the 83 vascular species found on the calcareous sand there are about 10 which practically never occur on chalk soil (Table VI, p. 231). There are some 5 others besides which I have not seen in chalk grassland or associated habitats of a kind analogous to those on the calcareous sand.

The real test of similarity with chalk grassland, however, lies with the constant species, which make up the bulk of the chalk grassland community. Of the 45 species of constancy 5, 4 or 3 recorded by Tansley & Adamson (i.e. occurring in 40 % or more of their South Downs areas) only 8 are absent from the calcareous sand (Table IV). This indicates a remarkably complete representation of the chalk grassland flora considering the smallness of the area.

[1] Recorded only from the calcareous Bargate Stone of the Lower Greensand, and "at Leaser's Barn, nr. Wotton" (Dunn, 1893). Leaser's Barn is about 0·4 km. from the calcareous sand area, so even if this record does not actually refer to the calcareous sand area here described, it shows that *Helianthemum* had already reached the locality from the chalk at least 44 years ago.

Table IV

Brackets explained in the text

	Constancy		Constancy
Avena pratensis	5	Phyteuma orbiculare	4
Asperula cynanchica	4	(Prunella vulgaris)	4
Plantago media	4	Primula veris	4
(Anthoxanthum odoratum)	4	Gentiana amarella	3

These 8 species are all common on the chalk escarpment of White Down, 1 km. from the calcareous sand.

These species, which, with the exception of *Anthoxanthum odoratum* and *Prunella vulgaris*, are absent from the Lower Greensand, might on the face of it be regarded as finding growth on the calcareous sand impossible owing to physical and not to chemical soil factors. This would, however, involve two unjustifiable assumptions:

(1) That all the commoner chalk grassland species would be found on a genuine chalk grassland under conditions the same, apart from soil, as those of the calcareous sand area.

(2) That they all have by now had ample opportunity to reach the calcareous sand from the neighbouring downs.

On the basis of Tansley & Adamson's constancy figures, which were calculated from areas of the same order of size as the calcareous sand area, *Avena pratensis* is the only one of the foregoing species for which there is a strong probability that condition (1) would be fulfilled. Considering that several species rarer on the neighbouring chalk than *A. pratensis* (e.g. *A. pubescens*) have fulfilled condition (2), it is reasonable to expect that *A. pratensis* has had the same opportunity for arrival. We may therefore provisionally conclude that a physical deficiency is preventing the occurrence of *A. pratensis* on the calcareous sand. It may be remarked that a notable physical disadvantage of the sand compared with the chalk is its liability to severer drought (see p. 233), but whether this fact is responsible for the absence of *A. pratensis* is by no means certain.

Comparison with Greensand flora

The number of species occurring on the calcareous sand is much larger than that on the acid sand. Taking the total flora of the calcareous sand, including the bare and the trampled areas, the numbers are 83 : 34. Considering only the grassland proper of the calcareous sand, the numbers are 60 : 34. There is no doubt that the greater variety of habitats on the calcareous sand, and the closer proximity of agricultural land, exert an influence towards raising the number of species on the grassland proper through the seed-parent effect; while the greater frequentation by people would also act in this direction on the whole. But bearing in mind the relative poverty in species of similarly frequented and disturbed areas in other places on the acid soil of the Folkestone

beds, it is quite certain that the difference in the number of species is due in large measure to the one soil being calcareous and the other not.

Species on the greensand, not on the calcareous sand nor the chalk

Turning now to the species occurring on the acid sand area but not on the calcareous sand (Table V), the prima facie argument applying to these would be that their occurrence on the Lower Greensand is influenced by chemical rather than physical factors, because they are absent from a soil which is a typical greensand physically, but not chemically.

Table V

Brackets explained in the text

Aira praecox	Ornithopus perpusillus
(Anthoxanthum odoratum)	Potentilla sterilis
Calluna vulgaris	Stellaria graminea
Deschampsia flexuosa	Trifolium filiforme
Galium saxatile	(Veronica officinalis)
Holcus mollis	Vicia augustifolia
Myosotis versicolor	

The unbracketed species in this table are not found in chalk grassland; those in brackets occur there not uncommonly. (*Anthoxanthum* and *Veronica* are, however, much less typical there than on the greensand.) *Potentilla sterilis* is known on chalk soils, but in woods, and not in types of habitat comparable with the acid sand area, i.e. it evidently competes in grassland on the greensand but not on the chalk.

Aira praecox is known elsewhere (e.g. Breckland) on calcareous sands, and to say from the present evidence that it is a chemically determined calcifuge is probably wrong. Since a false deduction has to be admitted in this instance, similar errors may be possible in other cases, and indeed one must allow a wide margin of error in dealing with this accidental "experiment". Nevertheless all the species in Table V are commoner on dry acid soils than on dry calcareous ones, and from the insight into the question provided by the presence of the calcareous sand area, it may provisionally be stated that for these species (except *A. praecox*) this preference is influenced by chemical soil factors. The present evidence does not indicate whether absence from the chalk is connected with physical soil conditions as well; the latter influence is, however, presumably not important in the case of those species which occur on leached chalk soils (*Anthoxanthum odoratum, Calluna vulgaris, Veronica officinalis*).

To this class may be added *Rumex acetosella*, which although occurring on the calcareous sand area is there restricted to spots with no free chalk. The species has been noticed growing in the presence of free calcium carbonate or of lime (Tansley & Adamson, 1925; Thomas, 1930; Summerhayes & Turrill, 1927; and other cases have been brought to my notice). In the first two of the quoted instances it was not in competition, and in the third it failed to flower. It is manifest that the species can grow in calcareous soils,

but on these it is apparently at a disadvantage in competition, and the occasional records of its occurrence on them in no way belies the conclusion derived from the calcareous sand area, that the disadvantage is at least partly chemical. It may appear surprising to include a species which can be found growing on chalky substrata as a "calcifuge" and it must be emphasized that this use follows the definition on p. 218.

Species on the greensand and the calcareous sand, not on the chalk

Of the following species which occur on the calcareous sand (Table VI), three are found on the acid sand area, all are known on some sort of habitat or another on the greensand (Brewer and Dunn), and all are absent or very rare on chalk or leached (acid) chalk soils. Tests were made round the roots with dilute hydrochloric acid, for all the species save *Sagina apetala*, of which only one plant was found so that conclusions about it are unwarrantable. Effervescence occurred in every other case except that of *Rumex acetosella*, which therefore is also to be omitted from discussion under this heading (see above).

Table VI

Brackets explained in the text

Erodium cicutarium	(Rumex acetosella)
Myosotis collina	(Sagina apetala)
Plantago coronopus	Saxifraga granulata
Potentilla argentea	S. tridactylites
Pteridium aquilinum	Trifolium arvense

It is to be supposed that one or both of the following factors contribute to the occurrence of these species (excluding the two in brackets) on the calcareous sand and not on the chalk:

(*a*) Although not favoured by a genuine chalk soil, free calcium carbonate and alkaline *p*H are at least tolerated if the soil is sandy, so that absence from the chalk is to be attributed to its unfavourable soil texture. This may be illustrated by reference to four of the species in Table VI.

Plantago coronopus does not compete inland except on trampled ground, but (in Surrey at any rate) only trampled ground on the coarse-grained soils (the sands and gravels). It is probable that the caked condition of trampled chalk or clay soil makes its growth impossible, but trampled sand always remains porous and penetrable, so that *P. coronopus* grows on it whether it is calcareous or not. As a matter of fact it is much more abundant on the calcareous sand than it is in similar habitats on the normal acid sands, so that it would appear that it is favoured considerably by a high *p*H and/or high base status, as is suggested by its special abundance in submaritime habitats. Thus *P. coronopus* would probably be a calcicole if chemical soil factors were alone concerned. As regards physical factors it prefers coarse-grained soils such as acid sands to fine-grained soils (including chalk). The physical require-

ments evidently exert the stronger influence in non-maritime habitats and so determine its inland distribution.

Potentilla argentea occurs on sands and gravels. Dunn states that on the Lower Greensand it is characteristic of the Folkestone beds but not the Hythe beds. The latter contain a considerably larger proportion of clay than the former, and, taken in conjunction with its presence on the calcareous sand but not on the chalk, this suggests that *P. argentea* is a species of acid sands or of calcareous soils, provided that they contain a high proportion of coarse as compared with fine soil fractions.

The same facts and arguments are true for *Saxifrage granulata*, which Dunn also gives as a species characteristic of the Folkestone beds.

Pteridium aquilinum, according to the evidence here presented, tolerates calcareous soils (although reduced in vigour) as long as the physical conditions are tolerable. Its extreme rarity on the chalk may perhaps be due to the hindrance its rhizomes would meet in the parent rock. I have seen specimens growing in a chalk spoil heap (where the parent rock is disintegrated) but they were not in competition, and were suffering from lime chlorosis (cf. those on the calcareous sand).

(*b*) The "seed-parent effect" may be partly responsible for the presence of some of the species of Table VI on the calcareous sand—i.e. they may be present on an area which is not really the right habitat for them simply because it is small and surrounded by the greensand, which is continually shedding seed of its own flora over the surrounded area.

For the majority of the species in Table VI, factor (*a*) (p. 231) is probably more important than (*b*), and we may reasonably regard most of them as owing their calcifuge habit (as between the chalk and the greensand) to physical rather than chemical soil factors.

Poa annua may properly belong in this section. It is locally abundant on the calcareous sand, but is not at all common on the chalk (Brenchley, 1912).

Comparison with Breckland

Watt (1936) mentions that some of the plant communities of the Breckland of East Anglia show affinities with the chalk grassland of the south of England, and others with communities of the adjacent Lower Greensand. Since sands occur in Breckland ranging from strongly acid to markedly calcareous and alkaline, one would expect to find an interesting field for comparison. The writer is familiar with the work of Watt on the Brecklands, and it is to be hoped that later some correlation of Breckland data with those in this paper may be possible. At present, however, exact information is too scanty to make a detailed discussion profitable. Questions of climate and biotic influence would have to be considered along with soil and flora.

Data kindly shown to me by Dr Watt prior to publication suggest that several of the species concerned in this paper behave in a similar way in respect

to soil factors in Breckland, while in the case of others there is superficial disagreement.

V. DROUGHT ON CHALK AND GREENSAND

Water availability in dry weather is likely to be one of the most influential physical differences between chalk and greensand soils. That the chalk is liable to less extreme drought than the sand might be inferred tentatively from the soil analyses given in Table A, which show the greater water-holding capacity of chalk soils; but this alone furnishes no proof that there is more water available to plants in dry weather.

A simple experiment was arranged to discover whether wilting occurred sooner on chalk soil or on greensand. A good opportunity for exact comparison was provided by the calcareous sand vegetation, because soil complete with turf could be obtained from it bearing the same species as turf from chalk grassland, in the same state of luxuriance.

The six samples of turf—three chalk and three calcareous sand—included soil to a depth of 25 cm. They were fitted into glazed pots and saturated with water at the start of the experiment, and then subjected to summer drought by standing them out of doors under a glass roof which kept off rain but permitted normal wind and temperature effects. After a month it was obvious that wilting was more serious on the sand.

This experiment tells one nothing of the supply of ground water coming up from a depth below 25 cm., but there is every reason to regard the chalk as the more plentiful reservoir. It may be concluded that in comparable situations drought is a more serious problem on the Folkestone beds of the Lower Greensand than on the chalk.

VI. SUMMARY

A small area, referred to as the calcareous sand, was found on the Lower Greensand in Surrey, within 1 km. of the chalk, bearing a herbaceous flora closely resembling that of chalk grassland. Only 8 of the 45 species of constancy 3 or over, recorded by Tansley & Adamson for chalk grassland, were absent from this flora—a remarkable fact considering the small size of the area. The soil contained chalk intimately mixed with the sand; it was probably scattered on the land for agricultural purposes more than 50 years ago.

An adjacent area on typical acid greensand soil, bearing a vegetation of the same general type as the calcareous sand, and subject to more or less similar physiographic and biotic conditions, was studied in order to use it as a rough "control experiment". The soils of the calcareous sand and acid sand areas hardly differ significantly in mechanical analysis fractions; they are both quite distinct from chalk grassland soil in this respect, but the calcareous sand is similar to it in pH and the possession of free chalk. Therefore comparison of

the flora of the calcareous sand with that of chalk grassland on the one hand, and of the acid sand (supplemented by other greensand records) on the other, affords a means of studying the respective importance of physical and chemical soil factors in determining the calcicole and calcifuge habit in a few of the species of the chalk and of the greensand respectively. The sense in which the words "calcicole" and "calcifuge" are used is defined in the Introduction. The observations in this paper refer only to dry soils, whether calcareous or acid.

The conclusion is reached that for the vast majority of chalk grassland species the factors determining the calcicole habit are chemical. This is in agreement with the view commonly held.

It has been possible to group some of the species into the following classes. The text must be consulted for qualifications applying to them. The meaning of the headings is amplified on p. 219.

Calcicoles determined by chemical soil factors:

Certainly the six species in Table III, e.g. *Avena pubescens*, *Bromus erectus*, *Helianthemum vulgare*; probably a good many besides those in the table (see text, p. 227).

Calcifuges determined by chemical soil factors:

Most of the thirteen species in Table V, e.g. *Calluna vulgaris*, *Deschampsia flexuosa*.

Calcifuges determined by physical soil factors:

Most of the ten species in Table VI, e.g. *Plantago coronopus*, *Saxifraga tridactylites*.

The available data do not make it possible to consider the very hypothetical class of "physically determined calcicoles".

Avena pratensis is the most important chalk grassland species absent from the calcareous sand, and it is considered likely that a physical soil deficiency is the reason for this. The chances of distribution are probably responsible for the absence of some other common chalk species.

Attention is drawn to the edaphic similarity of the calcareous sand to some of the soils of Breckland. Many of the species concerned in this paper occur there, and some appear to exhibit similar behaviour in relation to soil factors. Attempts at detailed correlation of the floras would, however, be premature on the present data.

A simple wilting experiment indicated that for grassland vegetation drought is a more serious problem on the Folkestone beds on the Lower Greensand than it is in similar situations on the chalk.

I am glad to express my indebtedness to Prof. A. G. Tansley, Dr A. R. Clapham and Dr A. S. Watt for information and criticism generously given on

many points, to Dr W. Watson for naming three of the cryptogams, to the staff of the Soil Science Laboratory, Oxford, for facilities given in carrying out the soil analyses there, and to Dr J. L. Russell for criticism of the work relating to the soil.

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REVIEWS

THE JOURNAL OF ANIMAL ECOLOGY

(Vol. 6, No. 2, November 1937)

This number (175 pages) contains fourteen original papers dealing with animal ecology in Great Britain, the Channel Islands, the Canadian Arctic, Ceylon, the Solomon Islands, Australia, the United States and U.S.S.R.; also seventeen reviews and 151 Notices of Publications on Animal Ecology.

Ecological surveys include R. J. A. W. Lever's study of the animal community living in *Themeda-Imperata* grassland on Guadalcanal Island, in the British Solomon Islands Protectorate. D. F. W. Baden-Powell gives an account of a Holocene shallow-water marine assemblage from a deposit just above sea-level in the west of Scotland, special attention being paid to the Mollusca and the Foraminifera (the latter being the subject of a report by W. A. Macfadyen).

The movements of animals and their choice of habitat occupy several papers. Orlando Park describes, from Illinois, the activity of a log-inhabiting beetle, *Passalus cornutus*, which is shown to be uninfluenced by day and night rhythms in its surroundings. A new form of audio-frequency recording apparatus is described, which has great possibilities for ecological experiments.

M. E. Solomon, along a rather different line, describes from Western Australia a long series of experiments with a terrestrial earth mite, *Halotydeus destructor*, designed to show how it moves in relation to optimum physical conditions, rejecting extremes and tending to come to rest at the optimum, with resulting aggregation of individuals. J. Laing proves, by clear-cut experiments with parasitic Hymenoptera, that the general surroundings of the host may be of equal importance with the host's own characteristics in determining the parasite's ability to find and recognize its host.

T. C. S. Morrison-Scott gives some evidence about the mutually exclusive distribution of two shrews on the Island of Jersey. In an important study of the races of wood-mouse (*Apodemus sylvaticus*) in the plains of Russia and the mountains of the Ante-Caucasus, N. J. Kalabuchov proves by transfers in the field, by laboratory experiments, and by blood investigations, that the physiological differences connected with life at different altitudes are partly fixed biological characters.

Population studies occupy several papers. B. T. Parsons and A. D. Middleton publish an up-to-date map showing the distribution and continued spread of the grey squirrel in Great Britain. Middleton, in another paper, records the state of the British partridge population in 1936, with notes on a sudden decrease observed in 1937. Helen Chitty and Middleton have a detailed analysis of adult partridge foods, showing the changes that occur with the march of the seasons and the cycle of agricultural operations. A count of the gannet population of Ailsa Craig (about 5945 nests) is given by H. G. Vevers, James Fisher, C. H. Hartley and Alan T. Best. K. D. Baweja contributes a suggestion for a convenient unit in soil population analysis. Notes on a parasite census of Ceylon bats are recorded by Gordon B. Thompson.

The populations of arctic foxes, snowy owls, lemmings, and also sledge dogs, living in the Canadian Arctic, are the subject of a report by Dennis Chitty and Charles Elton, who record the findings of a large-scale questionnaire enquiry for the season 1935–6, mapped by a new method.

Reviews deal with the *Journal of Ecology*, the natural history of Glamorgan, intertidal surveys, wild life conservation, the insects of trees, spring frosts, plant ecology teaching, marine biology of fish and oysters, and other subjects. The Notices of Publications on Animal Ecology, done by six workers, provide abstracts of most current research on animal ecology in the British Isles.

CHARLES ELTON.

FORESTRY

Forest Bibliography to 1933. Part I, pp. xviii and 78, price 5*s*. Part II, pp. 120, price 12*s*. 6*d*. Compiled and published by the Dept. of Forestry, University of Oxford, 1937.

This publication represents the references to forest literature accumulated by the Oxford School of Forestry and the Imperial Forestry Institute up to 1933. They give a fairly complete list of papers and other matter published in English up to that date, with a very considerable number in French and German. Few publications in other languages are included unless they include summaries in one of the three languages mentioned.

The classification adopted groups the references under such headings as General Forestry, Silviculture, Utilization, Mensuration, Geology and Meteorology. Ecological references come mainly under Silviculture and Forest Protection. This system is to be replaced, for references after 1934, by the decimal system of classification adopted in that year by the International Union of Forest Research organizations. A table collating the two systems is given in Part I, which also includes the references under General Forestry and Silviculture, (1) General—including forest types and ecology, (2) Seed and seedlings. Part II concludes the references on Silviculture (natural and artificial regeneration, maintenance, systems, and notes on Trees). Later parts will complete the publication.

W. H. P.

SOIL SCIENCE

Robinson, G. W. *Mother Earth, being letters on soil addressed to Professor R. G. Stapledon, C.B.E., M.A.* Pp. viii + 202, with 1 plate, 2 maps and 6 text-figures. London: Thomas Murby and Co. 1937. Price 5*s*. 6*d*.

This stimulating little book represents an intriguing attempt to write a book of general interest on soil science and its implications. It is written in the form of letters to Prof. Stapledon, who would certainly be a sympathetic recipient. Its form, contents and conclusions are such that it should be received with equal gratitude by a very wide circle of readers.

In outline, the book covers most of the subjects familiar in books on soil science. A mere recital of these topics would give an unfair idea of the character of the book, for Prof. Robinson writes of the soil not only as one who is interested in its scientific problems, but as one who sees in the proper conservation and utilization of soil the solution of many, if not of most, of the problems afflicting the modern world. The consideration of particular soil problems in relation to their general bearing and economic application is very well done.

Of equal and possibly of greater interest to ecologists, is the ecological outlook which is shown in the treatment. In this the book is a sign of the times, for the most interesting development of modern soil science has been its tendency to leave the laboratory and go out into the field. In a word, the pedologist to be fully effective has found it necessary to acquire also an ecological outlook. The chapters, which possibly possess greatest interest from this point of view, are those on humus, on soil profiles and on the typical soils of grasslands, forests and waste lands. Thus Prof. Robinson lays emphasis on the view that the soil profile "bears imprinted upon it the history of the soil. If we could only read it aright we could reconstruct

that history, just as an archaeologist can reconstruct the history of a site like that of Troy." His appreciation of this point of view is apparent in later pages. Thus he considers that many of the so-called "ffridd" lands in Wales (bearing *Agrostis-Festuca* pastures) occur only on ancient forest sites. From these the surface soil has been partly removed by erosion following forest destruction, thus accounting for their characteristic truncated soil profiles.

Great emphasis is also laid upon the role of humus in maintaining soil structure and fertility and hence stress is laid on the importance of the two processes of "humification" and oxidation, in any sound system of soil conservation. A number of examples, including that of North America, are given in illustration of the disasters which follow the uncontrolled exploitation of the humus reserves. In discussing this question, the author attaches great value to the introduction of grass "leys" into the crop rotation as a means of preserving soil structure and humus content. He also draws attention to the deterioration of soil conditions which may result from uncontrolled conifer plantings. His treatment of the bearing of the humus and soil structure problems upon colonial development should be familiar to all engaged in colonial administration.

W. H. P.

Rothamsted Experimental Station Report, 1936. Pp. 294. Price 2*s*. 6*d*. (Obtainable from the Secretary.)

This annual report fills a special place in the literature of science applied to agriculture. The present volume contains the customary survey of the present position of the various investigations on soil and fertilizer problems conducted at the station, together with pertinent data for the year. There is, moreover, a long-period survey dealing with the results of the field experiments.

Of more particular interest to those working on soil may be the survey (with full references) of the work done by the Department of Fermentation dealing with the chemistry and mechanism of decay of organic materials and with the factors which may affect it.

Similar summaries deal with entomology and insecticides. Summaries of the various scientific investigations published during the year are also given.

W. H. P.

BRITISH ECOLOGICAL SOCIETY

SUMMER MEETING AT WRAY CASTLE, WINDERMERE, 28 AUGUST—1 SEPTEMBER 1937

By the kind invitation of the Council of the Fresh-water Biological Association and of the Director of the Station, the Society was able to hold its Summer Excursion at Wray Castle, Windermere. The organization of the meeting was kindly undertaken by the President, Dr Pearsall. About twenty-five members were present: some were accommodated in the Castle and some in Ambleside.

28 *August*. After dinner in the evening there was an informal meeting in the library of Wray Castle. Dr Pearsall gave an account of the general ecology of the area. He pointed out that the rocks are of three main types, the Borrowdale slates which are very hard and give steep acute hills and shallow soil, the Bannisdale slates which are softer and which give lower hills of rounder outline, and a deeper soil, and in the north, the similar Skiddaw slates. There is much superficial drift, and some outcrop of limestone to the south of Windermere. A series of lakes of glacial origin vary according to whether they lie in the softer or the harder rocks. For example, Windermere, which is in the softer rock, shows more silting and a richer vegetation. The high rainfall causes soil leaching which is marked on the deep soils, and has pronounced effects on the vegetation, although it is offset on steeper slopes by the effects of weathering and downwash.

Dr Pearsall pointed out that the area round Windermere has the highest percentage of natural woodland in Britain, consisting mostly of *Quercetum sessiliflorae* in a nearly natural condition. Man has exploited the woods until about eighty years ago for charcoal for iron smelting, producing coppice with standards, containing abundant hazel, birch and ash. Later there was bobbin and gunpowder manufacture. The exploited woods are very mixed, but the native woods have only occasional holly and birch under the oaks. There has also been marked deforestation from 1800 ft. downwards, by sheep grazing on the hillsides, and it was pointed out that this may have begun in prehistoric times, because all Bronze Age remains occur at 1000 ft. or more, save on the exposed western faces where they go down to 500 ft. The grazing is mostly *Agrostido-festucetum*, with *Nardus* where the drainage is locally poor.

The Director of the Station, Dr Worthington, gave an introduction to the work going on in the laboratory, indicating how the production cycles in Windermere were being investigated from many different angles. He briefly indicated the chemical measurements made by Dr Mortimer on the dissolved and suspended substances in the Lake, their seasonal variation, and the recent detailed bathymetric survey of the lake by echo-sounding. He mentioned the work of plankton collection and algal culture, carried out by Dr Rosenberg, and the work of Dr Misra in relating rooted vegetation to the nature of bottom deposits. He showed that Misra's conclusion for plants had been extended by Mr Macan to water bugs, different species of which are associated with successive stages in the evolution of the lake-bottom deposits. Lastly he mentioned the work of Mr Allen on studies of the food and growth of fish, particularly of the perch in Windermere.

29 *August*. During the day the party had the opportunity of examining a long series of exhibits showing the work of the laboratory, and of discussing these with the staff. By duplicating the trip, it was made possible for all members of the party to take part in an excursion on the lake in the Station launch.

Lake Excursion

Dr Pearsall and Dr Worthington gave a demonstration of the method of measurement of light penetration into the lake water by means of a Bernheim photoelectric cell lowered on a boom away from the boat. They demonstrated the typical logarithmic fall of light intensity with depth below the surface, and it was explained how light penetration is correlated with density of phytoplankton. It was shown that in a sequence of dry summers the reserves of nutrients in the lake are depleted and light penetration is great, but that rainy seasons, or sewage effluents, cause high phosphates and high nitrogen, with high phytoplankton density and less penetration. It was said also that the depth of rooted submerged Angiosperms depends directly on the light penetration.

The standard method of making a plankton haul was then demonstrated, and specimens were taken back for examination in the laboratory.

Dr Pearsall explained the factors which controlled the distribution of littoral phanerogams. Places with no silt had no plants, with young silt, abundant plants, and with an old, highly evolved, very organic bottom, again no plants. These features were demonstrated in Pullwyke Bay, which shows both a time succession and a zonation. The zonation showed *Phragmites* on the gravel shore, then a belt of *Carex inflata* and then *Scirpus lacustris* or *Equisetum limosum* on organic mud. The more inorganic silts showed *Potomogeton alpinus*, *Sparganium minimum* and *Elodea* with reed swamp of *Phalaris* and *Phragmites*. The more organic soils carried *Lobelia*, and in the reed swamp, *Equisetum limosum*.

30 *August*. The party visited Roudsea Wood and the adjacent peat moss. The moss is a typical example of a raised bog which has been severely drained and burned. The sphagnum surface is quite dead, but it retains the typical pool and hummock topography. *Myrica*, *Calluna* and *Erica tetralix* are now dominant with *Scirpus caespitosus* and *Eriophorum vaginatum* abundant, birch seedlings are scattered very abundantly over the bog surface, and the sloping margin of the bog next to the wood is covered with subspontaneous pine-birch wood. *Pinus* and *Betula pubescens* are dominant but make an open stand, and *Sorbus aucuparia* is frequent. The shrub layer is a continuous sheet of very tall *Vaccinium myrtillus*. *Myrica Ilex*, and *Dryopteris dilatata* are occasional. These pine woods are on the edges of all the mosses, and Pearsall regards them as the relics of native woods; they grow on very highly oxidized and very acid peat of *p*H 2·8–3·2. *Pteridium* is local on disturbed and less acid soil of *p*H more than four, often with *Molinia*, *Hypnum cupressiforme* and *H. schreberi*. In residual wet places on the bog surface the following mosses were recognized, *Sphagnum papillosum*, *S. plumulosum*, *S. tenellum*, *Campylopus flexuosus*, *Dicranella cerviculata*.

Roudsea Wood itself showed a remarkably complex and interesting vegetation related to a striking alternation of limestone outcrops through deeper calcareous clay becoming locally more or less acid. On the clays the woods were of oak-ash type with oak standards and ash copice. *Betula*, *Alnus*, *Quercus robur*, and sycamore were present with *Rubus saxatilis*, *Paris quadrifolia*, *Melica uniflora*, *Convallaria majalis*. The deeper soils carry *Brachypodium sylvaticum* and *Mercuralis perennis*. The sharp limestone outcrops were dominated by *Taxus*, but also carried abundant *Alnus*, *Corylus*, *Fraxinus*, *Euonymus*, *Tilia cordata*, and *Sorbus aucuparia*, with mosses such as *Hypum molluscum* and *Neckera*, and *Convallaria* in the shallow soils.

Where the wood was traversed by a deep valley, an old arm of the sea, there was a wide deposit of alkaline peat maintained by calcareous drainage water. It showed a sequence from *Phragmitetum* through a tussock swamp of *Carex paniculata* to fen wood dominated by *Alnus* and *Frangula alnus*. In many places both the reed swamp and fen wood had been cut, giving the very characteristic fenland patchwork, with all the typical fenland species. On the drained and cut slopes of the valley, the fen peat had become acid, and was covered with

Molinia with *Deschampsia flexuosa* and *Galium saxatile*, or with tall *Pteridium*: *Alnus* and *Betula* were colonizing it rapidly.

On the far side of the valley was fairly primitive oak wood on slate, which had undergone some felling but no coppicing. There were no trees but oak, but there were occasional shrubs of *Ilex*, *Betula*, *Sorbus aucuparia*, and *Tilia cordata*. The shallower soils carried *Rubus*, *Deschampsia flexuosa*, *Galium saxatile*, *Luzula pilosa* and *Teucrium scorodonia*. On the deeper soils there was *Pteridium* with some *Scilla* and *Holcus*, and on the rocky outcrops *Vaccinium myrtillus* with characteristic mosses such as *Mnium hornum*, *Hypnum cupressiforme*, *Dicranum majus* and *Hylocomium loreum*. There were conspicuously more mosses and ferns on the north- and south-facing slopes.

From the wood the party made its way to the shore of the estuary which was bordered by fragments of sandy salt marshes. Locally these marshes gave indications of a transition through *Phragmitetum* into fresh-water fen. After tea the party visited a strip of woodland on thin dry peat about nine inches thick overlying estuarine silt. Here *Betula pubescens* was dominant, with *Acer pseudoplatanus* frequent and *Taxus* rare. On the floor *Dryopteris dilatata* and *Scilla* were abundant, and it was suggested that the fern was the chief peat former.

31 *August*. The zoologists of the party visited Stickle Tarn, a series of peat pools at altitudes from 500 to 2000 ft., and examined the transition from lowland to alpine fauna.

The botanical party was taken to Tarn Howes, on the margin of which they examined a small drainage bog containing a mixture of oligotrophic and eutrophic species. The lake, with water of low hardness, has a Desmid plankton and contains *Litorella*, *Lobelia*, *Elodea*, *Potomogeton natans*, and *Myriophyllum spicatum*. The party then followed the outflow stream from the lake down to the Ambleside-Coniston road, examining on the way the bryophytes of the stream bed, and the fragments of primitive woodland on the valley slopes. Submerged in the stream were *Fontinalis antipyretica*, *Eurhynchium rusciforme*, *Alicularia scalaris*, and *Scapania*. In the splash zone were *Porotrichum alopecurum*, *Brachythecium rivulare*. Abundant on rock slopes by the beck were *Hymenophyllum unilaterale*, *Plagiothecium undulatum*, *Dicranum majus*, *Hylocomium loreum*, on sloping *damp* rock surfaces were *Campylopus atrovirens* and *Rhacomitrium protensum*, and on rock surfaces with acid drainage water *Blechnum*, *Diplophyllum albicans* and *Sphagnum* (?) *quinquefarium*.

The fragments of primitive wood had a very open stand of *Quercus sessiliflora* with marginal *Betula alba*, and a small amount of *Sorbus aucuparia* and no shrubs, or sparse hazel or holly. There were abundant seedlings of *Betula*, *Sorbus*, *Fraxinus* and *Quercus*, but few seedlings were surviving. The ground was completely carpeted with vegetation, mostly mosses. The Phanerogams included *Vaccinium*, *Galium saxatile*, *Potentilla erecta*, *Deschampsia flexuosa*, *Melampyrum hians*, *Oxalis acetosella* and *Pteridium* and *Anthoxanthum* on deeper soils where the slope is less and the soil of pH about 4·0. The ferns included *Blechnum*, *Lastraea oreopteris*, *Dryopteris filix mas* and *Hymenophyllum unilaterale*. The mosses included *Dicranum majus*, *Hylocomium loreum*, *Plagiothecium undulatum*, *Polytrichum commune*, *Dicranum scoparium*, *D. fuscum*, *Hypnum schreberi*, *H. cupressiforme*, *Sphagnum* spp., and *Leucobryum*.

The party then ascended Tilberthwaite Gill. The scree contained *Cryptogramme crispa*, *Saxifraga aizoides*, *Asplenium trichomanes*. The gorge was densely clothed with a scrubby woodland containing abundant woody species, but very little oak. The party did not stay to examine the wood but climbed through it to the *Agrostis-fescue* pastures of the fell top, and as rain began to fall made their way down from the ridge to the Gill.

The sincerest thanks of the Society are due to those who made possible such an interesting and instructive excursion and most of all to the President, whose extraordinary knowledge of the ecology of the area was so unsparingly put at our disposal. We shall remember with great pleasure this most successful of excursions.

H. G.

ANNUAL MEETING AT THE BOTANY SCHOOL, CAMBRIDGE
7–9 January, 1938

Soirée in the Botany School

On the evening of Wednesday, 5 January, between eighty and a hundred members and guests were entertained at a soirée in the Botany School.

A large number of interesting exhibits was shown in the laboratory. Dr A. S. Watt showed a large portion of a bracken rhizome extracted and mounted to exhibit its rooting depth in the soil and its general morphology. This was supplemented by smaller specimens and diagrams. Dr D. H. Valentine showed herbarium and living specimens of British primulas, violas and *Potentilla reptans*, hermaphrodite female plants of *Glechoma hederacea*, and the two sexes of *Petasites vulgaris*, together with a map showing their distribution in the British Isles. Mr M. H. Clifford had set out a collection of mosses from the growing bog surface of the raised bog at Tregaron, Cardiganshire. Dr Butler demonstrated a hygrometer for measuring micro-humidity gradients at the surface of a transpiring leaf under different external conditions of macro-environment. He showed at the same time an evaporimeter for measuring the evaporating power of the air at different heights above, and at various points on, the leaf surface, under different atmospheric conditions. Dr V. M. Conway showed an auxanometer apparatus employed in the field to obtain continuous records of the extension growth of the leaves of *Cladium mariscus*, together with results showing the daily and seasonal drifts of such growth at Wicken Fen. Dr H. Godwin had put out exhibits showing peat samples from various types of blanket bog and raised bog found in this country, and lantern slides illustrating the appearance, structure, and communities of such bogs. In particular there were diagrams showing the stratigraphy of the large raised bog at Tregaron, Cardiganshire. There were also shown examples of the application of pollen-analysis technique to peat deposits at Tregaron, and from the submerged peat beds of the North Sea. Mr G. C. Evans demonstrated a field potometer of the type he employed in ecological measurements in the Nigerian rain-forest, and a controlled condition experimental chamber. Mr P. Falk showed an exhibit illustrating the ecology of central Iceland, a vegetation map of the eastern slopes of the volcano Snaefell, transects and photographs. Dr P. W. Richards put out photographs of vegetation of the Middle Atlas, Morocco, and an exhibit of the growth forms of Bryophyta in tropical rain-forest. Mr Martin showed a vegetation map of the Kalahari sands of Northern Rhodesia, and herbarium specimens from the area. There had also been set out an illustrated account of the itinerary of the Friday excursion, which included an air photograph showing the extinct course of the Little Ouse river meandering as a "roddon" through the peat fens.

The Annual Meeting

The twenty-fourth annual meeting of the Society was held in the Botany School, Cambridge, on the following morning, Thursday 6 January, at 10 a.m., the President, Dr W. H. Pearsall, occupying the chair. The minutes of the previous Annual Meeting were read and confirmed. The report of the Honorary Secretary was read and adopted.

Hon. Secretary's Report for the year 1937

The twenty-third Annual Meeting of the Society was held in the Department of Botany, University College, London, on 9 January. On the evening of Friday, 8 January, about ninety members and guests were entertained to a soirée in the Department, where an exhibit of wide interest had been arranged.

The Annual Meeting was held on the 9th, and after transaction of business six very interesting papers were read to the Society. The warm thanks of the Society are due to Prof. Salisbury and Hill, who gave us the use of their Department and made arrangements for us in the usual generous manner.

The Summer Excursion of the Society was held at the Freshwater Biological Station Laboratory, Wray Castle, Windermere, from 28 August to 1 September. About twenty-five members were present, and took part in excursions to the Lake, to peat bogs, woods and to the local mountain pastures. We are much indebted to the Director and staff of the Station, who spared no trouble to make the meeting so enjoyable, and particularly to our President, Dr Pearsall, who made arrangements for the meeting, and most competently led the excursions.

In the past year two numbers of volume six of *The Journal of Animal Ecology* have been published, appearing in May and November. They contained respectively 238 and 184 pages, thus maintaining the substantial dimensions reached by volume five. Thirty original papers were published with eleven plates, in addition to notes, notices and reviews. Notices of publications on Animal Ecology in this volume totalled 307.

Since the last Annual Meeting there have been issued two numbers of *The Journal of Ecology*, appearing in February and August, and containing respectively 288 and 290 pages, with twenty-five plates. In this volume have been published twenty original papers, as well as notes and book reviews.

The end of this year is marked by the resignation of Prof. Tansley from the editorship of *The Journal of Ecology*. He has edited the *Journal* since the retirement of Dr Cavers. In his capable hands the *Journal* has steadily increased in size and importance, and the Society owes him the profoundest gratitude for his long and valuable service.

The Society's transplant experiments at Potterne are continuing satisfactorily in the hands of Mr Marsden Jones and Dr Turrill.

Since the last Annual Meeting the membership of the Society has risen from 343 to 350. Fourteen members have resigned or have died, and 21 new members have been elected. Of the present membership list 189 members receive *The Journal of Ecology* alone, 111 *The Journal of Animal Ecology* alone, 50 receive both *Journals* and one neither.

During the year the Council of the Society has been asked to interest itself in the National Parks movement, and it has sent representatives to committees called to advance the objects of this movement.

Dr Burtt Davy then spoke of Prof. Tansley's work as editor of *The Journal of Ecology*, paying tribute to the devotion and care with which he had carried out his duties. A vote of thanks to the retiring editor was carried with acclamation. The following elections and resignations were proposed from the chair, and carried *nem. con.*: elected new members, Messrs Dundas, Hope-Simpson, Piemeisel, Burges, Harley, Miss Carey, Mrs Brindley, the Wellington School Natural History Society: resigned, Messrs Eden, Longstaffe, Blair, Gilbert, and Pledge.

The alterations of rules proposed by the Council were explained by the President and Hon. Secretary, and being put from the Chair, were carried *nem. con.* They are as follows:

Rule 8 to read: "The Society shall be governed by a Council of not less than fifteen, and not more than twenty Members, consisting of the Officers of the Society, namely, the President, two Vice-Presidents, the two Hon. Editors, the Hon. Secretary, the Hon. Treasurer, and the Hon. Assistant Treasurer, with ordinary Members of Council."

Rule 14 to read: "The Hon. Assistant Treasurer shall be responsible for collection of subscriptions, shall assist the Hon. Treasurer, shall hold office for three years, and shall be eligible for re-election."

The meeting then proceeded to the election of officers as follows:

President: Prof. A. G. Tansley, F.R.S. (retiring, Dr W. H. Pearsall).

Vice-President: Dr A. C. Hardy (retiring, Prof. Salisbury).

Hon. Editor Journal of Ecology: Dr W. H. Pearsall (retiring, Prof. Tansley).

Hon. Editor Journal of Animal Ecology: Mr C. S. Elton.

Hon. Secretary: Dr H. Godwin.

Hon. Assistant Treasurer: Dr A. S. Watt. (See changes of rules proposed.)

Ordinary Council Members: Dr A. R. Clapham, Mr G. H. Bates, Dr E. W. Jones, Mr C. Diver, Mr A. D. Middleton, Dr F. T. K. Pentelow.

Retiring: Dr Leach, Prof. Boycott, Mr Wilmott.

Not retiring: Prof. Salisbury, Mr Oldham, Dr Russell, Dr Ashby.

Dr Pearsall then retired from the chair, and said in so doing how happy the Society was to welcome back to that office Prof. Tansley, who had been its first President, twenty-five years ago. Prof. Tansley, taking the chair, thanked the Society for the honour done him.

The Secretary then outlined suggestions for a single-day meeting at Bedford College at Easter, and for a Summer Excursion at Aberystwyth.

In the absence of further private business the meeting proceeded to the reading of papers.

Capt. C. Diver described the origin and purpose of the Association for the Study of Systematics, and explained what the Handbooks Committee of that body was doing to correlate the work of Ecology, Genetics, and Cytology with Taxonomic work. He asked for the support of the Society.

Mr J. Dundas read a paper on "Vegetation changes in the Sahelian zone of the southern Sahara". He described three main types of vegetation: Savanna thornland, Acacia scrub on indurated soils, and Fringing Forest on the damper soils by water courses. He also described the vegetational zonation round Lake Chad, an interesting example of regeneration of Acacia round new wells, and the marked association of *Tamarindus indica* with the baobab tree. A lively discussion followed, in which Dr Burtt Davy, Dr Godwin, Dr Burges, Mr Middleton, Capt. Diver, Prof. Tansley and Prof. Osborn took part.

Mr J. Ford then read a paper on the food of young partridge chicks, describing the results of crop-analyses from birds of different ages. There was an extremely well-marked change in diet at the end of three weeks, from entirely animal to largely vegetable food. He concerned himself mostly with analysis of the animal food, and drew attention to sources of error in interpreting results based on too few indices of presence. There was evidently much individual variation between birds caused by differing season and opportunity. Capt. Diver, Mr Middleton, Mr Wilmott, Dr Turrill and Mr Blackman took part in the discussion which followed.

Mr J. D. Martin then gave an account of the Baikiaea plurijuga forest and other vegetation types of the northern extension of the Kalahari Sands into North Rhodesia. The area lies north-west of the Livingstone Falls, at an altitude of 3000–3500 ft., and has very uncertain rainfall. The soils vary greatly in respect of the relative proportion of fine and coarse materials in them, and therefore in water-retaining power. It was shown how this affected vegetational distribution. Particular interest attaches to Baikiaea plurijuga, the dominant of one extensive forest type, since it is a deciduous, tap-rooted species of a genus otherwise limited to tropical (evergreen) rain-forest. Mr Martin suggested that this forest type had formerly been more widespread than at present, attributing this to climatic change, accelerated by fire, grazing etc. Dr Burtt Davy and Prof. Adamson spoke in the discussion after the paper.

Dr Burtt Davy then opened a discussion on nomenclature of Forest Communities in the Tropics. He indicated the conflict between existing systems such as those of Chipp and of

Champion, and circulated a draft conspectus for the African forests. The discussion which followed revealed both strong feeling that standardization would be extremely useful, and also a desire not to make premature commitments in instances where principles were not yet understood. Prof. Adamson, Dr A. S. Watt, Dr Richards, Prof. Osborn, Mr Wilmott and Mr Day spoke in the discussion. The meeting finally approved the proposal of the Hon. Secretary that the matter be referred to the Council for consideration by a special committee.

After the adjournment for lunch, the Hon. Treasurer made a provisional statement of the financial position of the Society. This was accepted as satisfactory, and a vote of thanks to the Hon. Treasurer, proposed by the President, was carried unanimously.

It was proposed from the chair, and carried *nem. con.*, that Messrs William Norman and Son be reappointed auditors for the ensuing year. Grants of £5 to the Transplant Experiments of the Society, and of £10 to the Freshwater Biological Association, were similarly approved.

Dr P. W. Richards then gave an account of stratification in a tropical rain-forest with only a single dominant. It was based on work done by Mr T. A. W. Davis of the British Forestry Department, Guiana. Dr Richards showed that the general characteristics of irregular outline, and stratification of woody plants into three or more layers, which is typical of mixed rain-forest, give place to smooth canopy and two storeys of woody plants where there is dominance by a single species. The President and Mr Holttum raised questions afterwards.

Mr P. Falk continued with an illustrated account of the Ecology of Central Iceland. He described mountain slope vegetation on lava soils at about 2000 m. He showed the pronounced effects of varying slope and soil depth, and of snow duration upon the vegetation. The reality of solifluction phenomena was demonstrated by ash-bands due to the volcanic eruption of 1783. In the wetter areas interesting examples of pool and hummock formation were described and the discussion, which followed, turned largely upon this. Mr Marquand, Mr Wilmott, Dr Polunin, Dr Clapham and Dr Turrill spoke.

Dr A. S. Watt then gave an account of some aspects of the autecology of the Bracken fern, concerned with excavation of the rhizome system. He showed how the system is a series of lateral shoots, produced in zig-zag fashion, and though small plants 88 and 68 ft. long had been measured, in another one lateral alone had produced over 200 ft. of rhizome. Dr Watt described the changes of density and rhizome depth across the invasion front of an area of bracken, correlating this with the appearance of the community. In the discussion the President, Mr Baker, Mr Summerhayes, Mr Montford, Dr Turrill, Capt. Diver and Mr Wilmott spoke.

Dr W. H. Pearsall then proposed on behalf of the Society very sincere thanks to Prof. Brooks for having given the hospitality of his department, and for providing the evening soirée. This was carried with acclamation. Dr Pearsall also thanked the Secretary and his assistants for the trouble taken in arranging the meeting.

On the following morning, a party of thirty, under the leadership of Dr Godwin and Mr Tidmarsh, made an excursion by 'bus through the south-eastern fens and the Breckland margin. In the fenland special attention was called to the buried pine forest horizons, the upper and lower peats separated by fen-clay, and the large silt "roddons" which represent the course of extinct rivers in Romano-British to pre-drainage times. The party crossed the Fen-Breck margin between Kenny Hill and Lakenheath, and had lunch on Maidscross Hill overlooking Lakenheath Warren. During lunch Mr Tidmarsh explained the communities visible, and the party then walked across the heath to meet the 'bus on the Brandon road. The party reached Cambridge just after 2.30 p.m.

	£	s.	d.	£	s.	d.	£	s.	d.
Subscriptions received, including arrears				516	18	1			
Less Prepayments for 1938–9				27	5	0			
				489	13	1			
Less Transferred to *Journal of Animal Ecology* (see below)				195	2	6			
							294	10	7
Interest on Investments				34	10	0			
Interest on Deposit Account				1	0	4			
							35	10	4
Journal of Ecology—Sales, etc.:									
Current volume, XXV, 1937				561	18	6			
Back volumes and parts				41	15	1			
Sales of reprints				65	9	6			
Fee for use of photograph				1	1	0			
				670	4	1			
Grants received from:									
University of London	40	0	0						
Ministry of Agriculture and Fisheries	10	0	0						
Government of Mauritius ...	50	0	0						
				100	0	0			
							770	4	1
Index Volume, *Journal of Ecology* (vols. I–XX), Sales							30	18	0
Journal of Animal Ecology—Sales, etc.:									
Vol. VI, 1937: Subscriptions received				195	2	6			
Sales				227	5	7			
Sales of reprints				39	13	9			
Vols. I–V: Sales of back numbers				98	6	10			
				560	8	8			
Grant from Carnegie Corporation of New York, through the Bureau of Animal Population, Oxford University				10	0	0			
							570	8	8
							£1701	11	8

	£	s.	d.	£	s.	d.
Working Expenses:						
Printing, Circulars, etc.	4	12	0			
Postages	8	3	8			
Bank Charges		16	2			
Clerical Assistance (Secretary and Treasurer) ...	15	0	0			
				28	11	10
Audit Fee				3	3	0
Grant:						
British Ecological Society's Transplant Experiments Fund				5	0	0
Soirée Expenses				3	7	11
Journal of Ecology, vol. XXV (1937):						
Paper, Printing, Illustrations, etc.	736	1	0			
Binding	2	1	0			
Carriage, Insurance, Postages, etc.	48	14	3			
Publishers' Commission	84	4	6			
				871	0	9
Index Volume, *Journal of Ecology*, vols. I–XX:						
Carriage, Insurance, Postages	6	12	7			
Publishers' Commission	3	1	10			
				9	14	5
Journal of Animal Ecology, vol. VI (1937):						
Paper, Printing, Illustrations, etc.	508	13	3			
Publishers' Commission	49	3	3			
Carriage, Insurance, Advertising, etc.	27	11	9			
Fee for Special Review	5	0	0			
				590	8	3
				1511	6	2
Balance, Surplus for the Year				190	5	6
				£1701	11	8

BALANCE SHEET AT 31 DECEMBER, 1937

Liabilities

	£	s.	d.	£	s.	d.
Membership Subscriptions, prepaid for 1938, etc....				27	5	0
Journal of Animal Ecology, vol. VI, pt. 2:						
Printing Account due	221	8	7			
Less Sale of reprints	24	7	6			
				197	1	1
Library Account				1	5	0
General Revenue Account, Balance of Funds:						
Balance at 31 December 1936	897	5	9			
Add Surplus for year ending 31 December 1937	190	5	6			
				1087	11	3
				£1313	2	4

Assets

	£	s.	d.	£	s.	d.
Westminster Bank—Credit Balances:						
Current Account	47	9	4			
Deposit Account	350	0	0			
				397	9	4
Investments:						
£700 3½ % War Loan at cost (Market value at 31 December 1937 at 101½ = £710. 10*s.* 0*d.*) ...	717	3	0			
£200 5 % Conversion Loan at cost (Market value at 31 December 1937 at 114½ = £229)... ...	198	10	0			
				915	13	0
				£1313	2	4

Audited and found correct and as shown by the Account Books of the Society. The Bank Balances have been verified by Bank Certificates.

(Signed) WM NORMAN & SONS.
Chartered Accountants.

120, Bishopsgate, London, E.C. 2.

Note. A further asset is the unsold Stock of the *Journals* and Index Volumes, held for the Society by the Publishers.

(Signed) HUGH BOYD WATT,
Hon. Treasurer.

LIST OF MEMBERS (January 16th, 1938)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, Dr H. Godwin, Botany School, Cambridge.

E. A. **Adams**, Dr Charles C.; New York State Museum, Albany, N.Y., U.S.A.
E. **Adamson**, Prof. R. S., M.A.; The University, Cape Town, S. Africa.
A. **Alexander**, W. B., M.A.; University Museum, Oxford.
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A. **Allee**, W. C.; Zoology Building, University of Chicago, Chicago, Ill., U.S.A.
E. **Allorge**, Pierre; Laboratoire de Cryptogamie, 63, Rue de Buffon, Paris.
E. **Alun-Roberts**, R.; Agricultural Dept., University College, Bangor.
E. **Anand**, P. L., M.Sc.; Dept. of Biology, Sanatana Dhanna College, Lahore, India.
E. **Andersonian Naturalists' Society** (cf. Glasgow).
E. A. **Arkwright**, J. A., M.D., F.R.S.; Lister Institute, Chelsea, London, S.W. 1.
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E. **Bates**, G. H., B.Sc.; The Farm Institute, Penkridge, Stafford.
E. A. **Beauchamp**, R. S. A., B.A.; The Laboratory, Wray Castle, Ambleside.
E. **Bell**, Prof. H. P.; Dalhousie University, Halifax, Nova Scotia.
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E. **Cowles**, Prof. H. C.; University of Chicago, Chicago, Ill., U.S.A. (*Hon. Life Member*).
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AN APPRECIATION

BY E. J. SALISBURY

BY the death of Arthur Edwin Boycott, at the early age of sixty-one, science has lost a distinguished pathologist and a naturalist of outstanding ability, whilst, for those who knew him well, there has passed from the scene a rich and scholarly personality whose friendship it was a privilege to enjoy.

The second son of a Hereford solicitor, Boycott was born in a district wealthy alike in its geological diversity and in the variety of its flora and fauna. Moreover, about the time that he was attaining maturity the Woolhope Club was at the zenith of its activity in the study of Natural History. On the excursions of the Club, Boycott, whilst still at the Cathedral School, came in contact with kindred spirits and particularly E. A. Bowles, who interested him in the Mollusca. At the age of seventeen he published a catalogue of the snails of Herefordshire, and this was the prelude to a lifelong interest in the subject of geographical distribution which in later years led to his editing the Roebuck Memorial number of the Conchological Society (1921), in which the data collected by W. Denison Roebuck were embellished by distribution maps, of all the British land and fresh-water Mollusca, which had been prepared by Boycott.

From Hereford Boycott went to Oriel College as a classical scholar and subsequently to Brasenose whence he obtained a first in the Natural Science Honours School. He subsequently went to St Thomas's Hospital and later to the Lister Institute.

From 1912 to 1915 he occupied the Chair of Pathology at Manchester University, where he came in contact with that peerless field naturalist, Charles Oldham. In 1915 Boycott was appointed to the Graham Professorship of Pathology in the University of London, tenable at University College Medical School, and at the same time came to live at Radlett.

In his new environment he quickly became an active member of the Hertfordshire Natural History Society and a regular attendant at its meetings, which were enriched by his gift for discussion and enlivened by his whimsical humour. At this time the H.N.H.S. included amongst its active members Dr Cook, the authority on Radulae, whilst C. Oldham, with whom the writer was privileged to serve as joint Hon. Secretary, was now as distinguished an authority on the Mollusca, especially that critical genus the *Pisidia*, as upon the habits of British birds. Boycott thus enjoyed the stimulus of sympathetic contacts and found time not only to pursue his professional duties and to edit devotedly for more than a quarter of a century the *Journal of Pathology*, but

to extend his studies of the habits and distribution of snails. The latter led him in 1918 to deliver as his Presidential Address to the Hertfordshire Society an account of the fresh-water Mollusca of the parish of Aldenham. This paper is a tribute alike to his industry and scholarship as also to his love of numbered paragraphs and footnotes. Some years later this account was supplemented by the results of further study in a second paper, and his Presidential Address to the British Ecological Society in 1933 was an extension of the same theme.

Boycott's tall figure, lean almost to emaciation, and clear-cut features were no more striking than his colourful personality. A man of strong views strongly held, he regarded any sort of compromise in respect to these as a betrayal of principle, though it were to the detriment of the causes which he espoused. To those who chiefly encountered his prejudices the marked capacity he had of exercising balanced judgement on scientific matters sometimes came as a surprise, whilst the very human and essentially kindly disposition beneath, that never spared itself in the service of others, was apt to remain unsuspected.

Boycott was at his best and happiest when tramping the country, which he loved with a discriminating appreciation, clad in an old suit of clothes and canvas shoes that, as he himself would put it, allowed water to drain away as fast as it had entered, and armed with a snail scoop. Thus equipped, with a tacit agreement to avoid the more controversial topics, he was the most delightful and charming of companions, as ready to learn as to impart, and as ready to apprehend phenomena of which he knew little as those of which he knew much.

Boycott's contributions to pathology were both numerous and distinguished, whilst his biological researches were no less able, but it was perhaps his passion for knowledge and his marked capacity to visualize it as a whole, rather than as so many abstractions, that marked him out from so many of his contemporaries.

STUDIES IN THE PERIODICITY OF THE ALGAE IN BEAUCHIEF PONDS, SHEFFIELD

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(*With five Figures in the Text*)

Introduction

Beauchief ponds lie on the southern outskirts of the City of Sheffield behind the ancient abbey of Beauchief. They form a series of three pools which are fed by a stream and communicate with each other when the water-level is high (Fig. 1). The two upper ponds have from time to time been cleared of weeds but the lowest pond on which these observations were made has been relatively undisturbed for many years. It was originally the fish pond of the monks at the abbey.

The pond has an area of 2000 sq. yd. and is nowhere more than 4 ft. deep. Considerable shade is thrown from the west by trees and from the east by a hawthorn hedge. The sides are steep and there is little littoral vegetation, but up to 1935 the bottom of the pond was covered by *Elodea canadensis* with local patches of *Potamogeton natans*. Early in that year the *Elodea* began to appear unhealthy, bearing very few leaves, and by the summer of 1936 it had almost disappeared.

The basin of the pool lies in an area of Millstone grit, but the bottom is everywhere covered with a thick layer of black mud made up mainly of organic detritus. The water supply comes partly from the overflow of the upper ponds and partly from drainage water from the surrounding farm lands. At the lower end there is a dam over which water escapes into the stream below, except when the water-level is low.

For some years Beauchief ponds have provided a useful collecting ground for algae. It was in an attempt to trace the cause of the very marked fluctuations in the commoner species that the present investigation was undertaken.

Methods

Samples of algae were taken every fortnight from various parts of the pond at a point about 5 ft. distant from the edge. In the frequency graphs only those algae are shown which were at some period abundant. In the alternate week, i.e. once a fortnight, water from two sides of the pond was taken back to the laboratory and analysed the same day for nitrate, phosphate, albuminoid ammonia, free and saline ammonia, silica and oxygen content. Records were

kept each week of temperature, hydrogen-ion concentration, water-level, sunshine and rainfall.

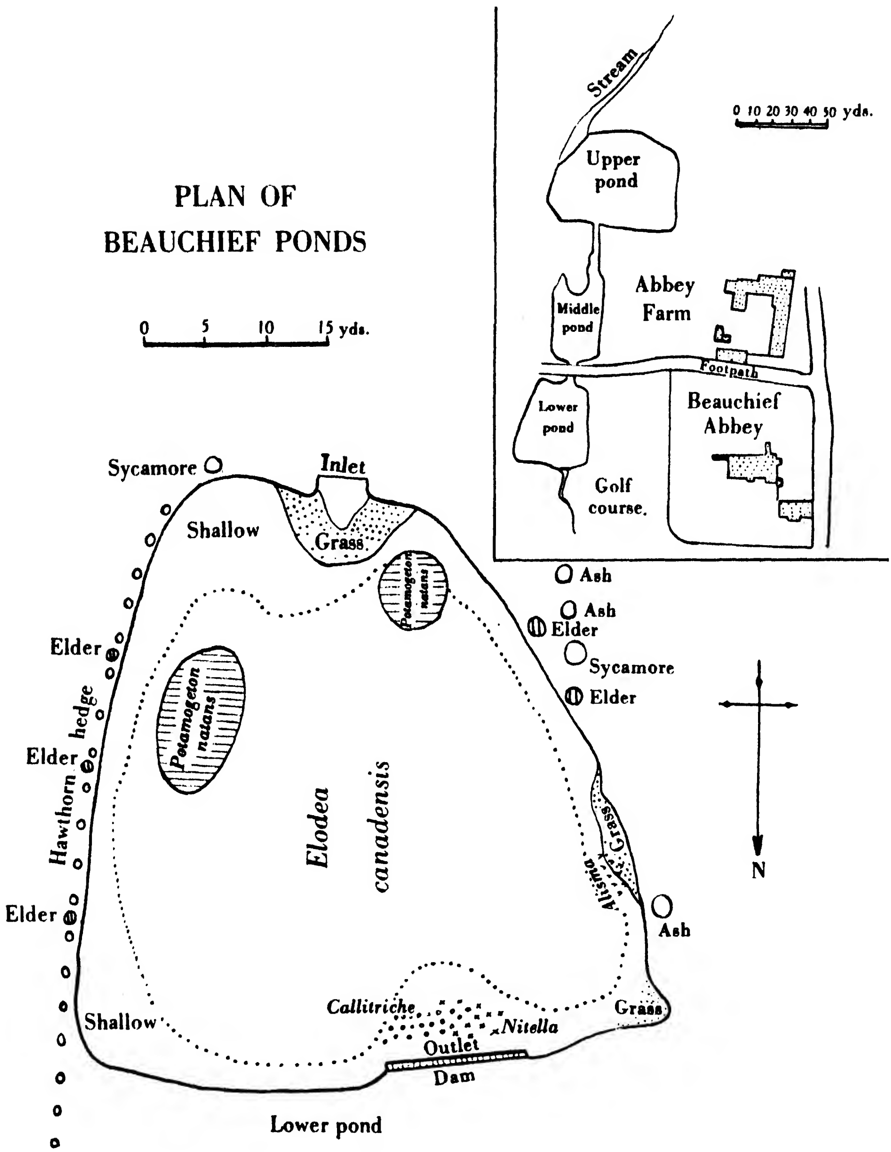

Fig. 1. Plan of lower pond at Beauchief ponds, Sheffield, with inset map showing its situation.

The water was taken each time from just below the surface of the pond. In such a shallow body of water it seems likely that the effect of wind and of the

flow of water from inlet to outlet would combine to prevent any appreciable stratification, except possibly during the dry summer months.

METHODS OF ANALYSIS

Nitrate. The phenol-sulphonic acid method was used and the colours were compared by means of a colorimeter (Purvis & Hodgson, 1922).

Ammonia, free and saline. 500 c.c. of pond water were distilled in a round-bottomed flask with sodium carbonate, the whole apparatus having been previously freed from ammonia. All the free ammonia was found to come over in the first 200 c.c. of distillate.

Albuminoid ammonia. To the remainder of the water in the flask, 50 c.c. of hot alkaline permanganate were added and the distilling continued until the distillate gave no colour with Nessler's solution. 2 c.c. of Nessler's solution were added to 100 c.c. of each of the first and second fractions and the colours compared with those given by a standard solution of ammonium chloride. Comparison was made in tall graduated glass cylinders (Purvis & Hodgson, 1922).

Phosphate. The method used was Florentin's modification of Deniges (Atkins, 1923 *a*). To each 100 c.c. of pond water were added 5 drops of freshly prepared stannous chloride and 2 c.c. of a solution composed of 100 c.c. 10 % ammonium molybdate and 300 c.c. of 50 % by volume sulphuric acid. The colours were compared in tall graduated glass cylinders with those given by varying concentrations of a standard solution of sodium ammonium hydrogen phosphate.

Silica. To each 100 c.c. of water to be tested were added 2 c.c. of 10 % ammonium molybdate and 4 drops of 50 % by volume sulphuric acid. The colours were compared against a picric acid standard (Atkins, 1923 *b*).

Oxygen. Winkler's method was used. The manganous chloride and alkaline KI were added at the pond to water contained in bottles of 285 c.c. capacity. The hydrochloric acid was added in the laboratory and the titrations carried out within half an hour of collecting the water.

Temperature measurements were taken 6 in. below the surface about 10.30 a.m.

Hydrogen-ion concentration was estimated colorimetrically, the tests being carried out in the field.

Water-level is expressed as the number of inches to which the water fell below the top of the dam.

RESULTS OF ANALYSIS

Nitrate. The monthly average of nitrate from September 1933 to August 1936 is shown in Fig. 2B. With the exception of 1936, the nitrate remained below 0·1 mg. N per l. throughout the summer months, becoming negligible in August. In October it began to rise sharply to a maximum reached in December

and then fell off again to reach a low figure in June. This general seasonal rise and fall may naturally be associated with depletion of nitrate due to the demands of phanerogams and algae during the summer months.

Each year there were secondary maxima always associated with heavy rain or melting snow which bring into the pond drainage water charged with nitrate from the surrounding farm land. A comparison of the nitrate curve with those for rainfall and water-level shows the close correlation which exists. The high nitrate of the summer of 1936 was again associated with high rainfall (Fig. 3B).

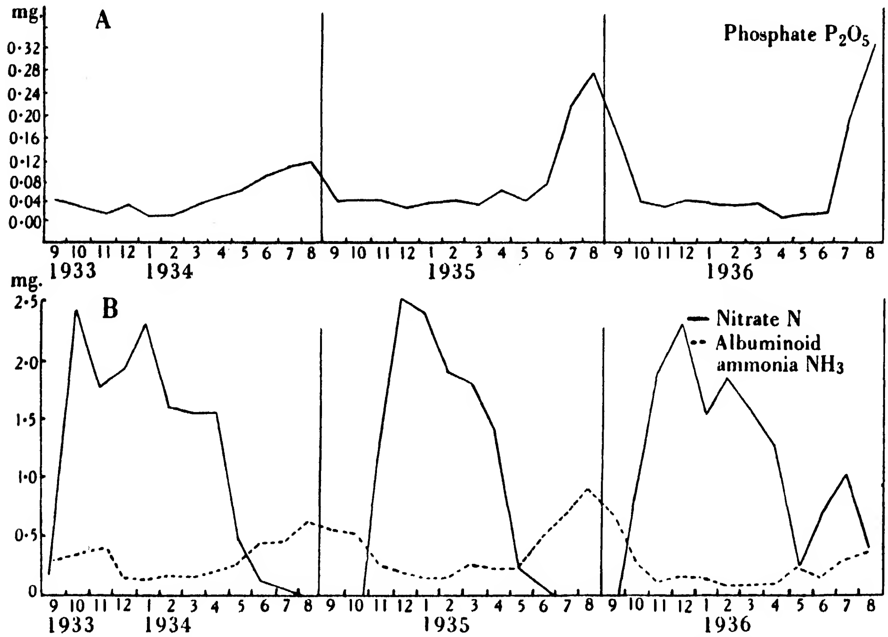

FIG. 2. Curves showing variation in A, phosphate (P_2O_5); B, nitrate (N) and albuminoid ammonia (NH_3). Expressed as mg. per litre.

Albuminoid ammonia. It was considered that the measurement of albuminoid ammonia would give some indication of the amount of decay going on in the pond and resulting in the return to the water of the products of protein decomposition. The maximum was reached each year in August (Fig. 2B) at a time when mats of filamentous algae were beginning to decay and phanerogamic vegetation was on the decline. The curve follows closely that for water temperature (Fig. 3A). In the summer of 1936 there was little alga in the pond to decay and a rather low sunshine record. These two factors would probably account for the summer maximum of only 0·35 mg. as compared with 0·9 mg. in the previous warm summer when dense mats of *Oedogonium* filled the pond.

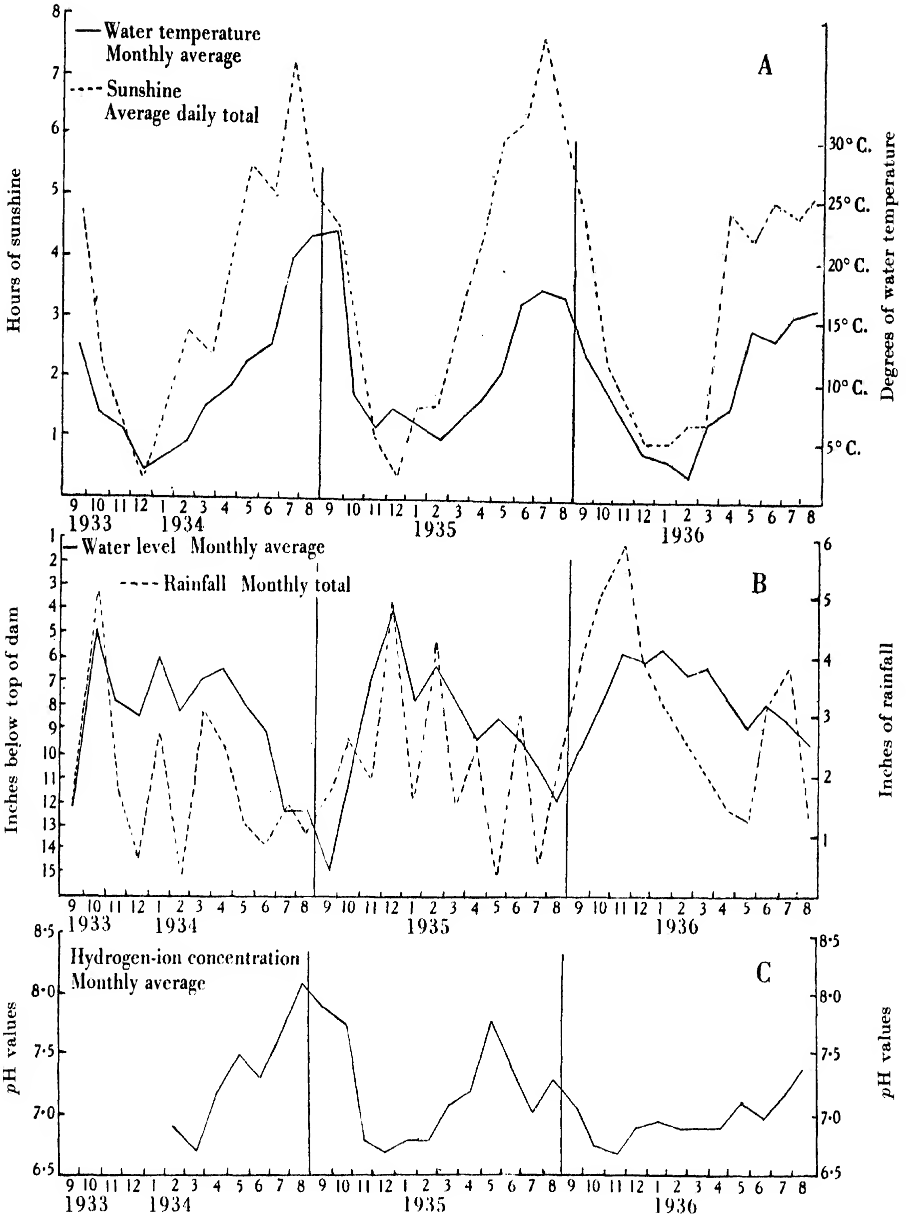

FIG. 3. Curves showing variation in A, water temperature and sunshine; B, water-level and rainfall; C, hydrogen-ion concentration.

Free and saline ammonia. This never exceeded 0·01 mg. per l. except after heavy rain or melting snow when farm washings were brought into the water.

Phosphate. With the exception of a marked rise in the summer the phosphate content remained fairly constant at about 0·03 mg. per l. (Fig. 2A). This figure is much higher than that found in larger bodies of water such as the English Lakes (Pearsall, 1930) and greater than that described for other freshwater pools (Atkins & Harris, 1925). The secondary maxima which show in the monthly average are due to unusually high readings over short periods. Inflow of drainage water had little effect on the phosphate content of the water and the summer maximum as well as local increases must be due to internal causes. It is doubtful if decay of vegetation alone is sufficient to bring about the pronounced increase in phosphate in July and August. On one occasion dead fish were noticed and may have been a contributory cause. Twice, the local rises followed periods when the pond was frozen, but the prolonged frost of 1936 had no appreciable effect.

In 1934 and 1935 a distinct rise followed the spawning of frogs in April. In 1936 disaster overtook the frogs before much spawn had been laid and there was no increase in phosphate.

Increase in phosphate did not appear to affect the growth of the algae in the pond and there was no indication that lack of phosphate acted as a limiting factor (Atkins, 1923 *a*).

Hydrogen-ion concentration. The *p*H of the pond lies between 6·7 in winter and 8·1 at the height of summer (Fig. 3C). The curve follows closely that for sunshine (Fig. 3A), suggesting that changes in *p*H are largely due to the photosynthesis of vegetation in the pond. The fact that the fluctuations were small in the summer of 1936 bears out this idea, for although the sunshine increased considerably in April of that year there was little *Elodea* and only a poor growth of algae. It may be significant that the *p*H decreased at a time of maximum sunshine in July 1935 (Fig. 3A) when there was much decay of algal vegetation.

Silica. Figures for silicate were obtained for 1 year only. The lowest value was 3 mg. SiO_2 per l. and the highest figure of 7·15 mg. was reached after heavy rain.

Oxygen content. This did not vary very greatly during the 1 year for which figures are available. The lowest figure of 1·2 parts per 100,000 was reached in January and the highest of 2·71 the following month.

Periodicity of algae

Volvox aureus Ehr. This coenobiate alga showed a winter maximum in December or January and a summer maximum in August or September. Hodgetts (1922) found a temperature of 6–12° C. to be favourable to *Volvox*, and Knoke (1924) suggests that it grows best in warm sunny weather. At

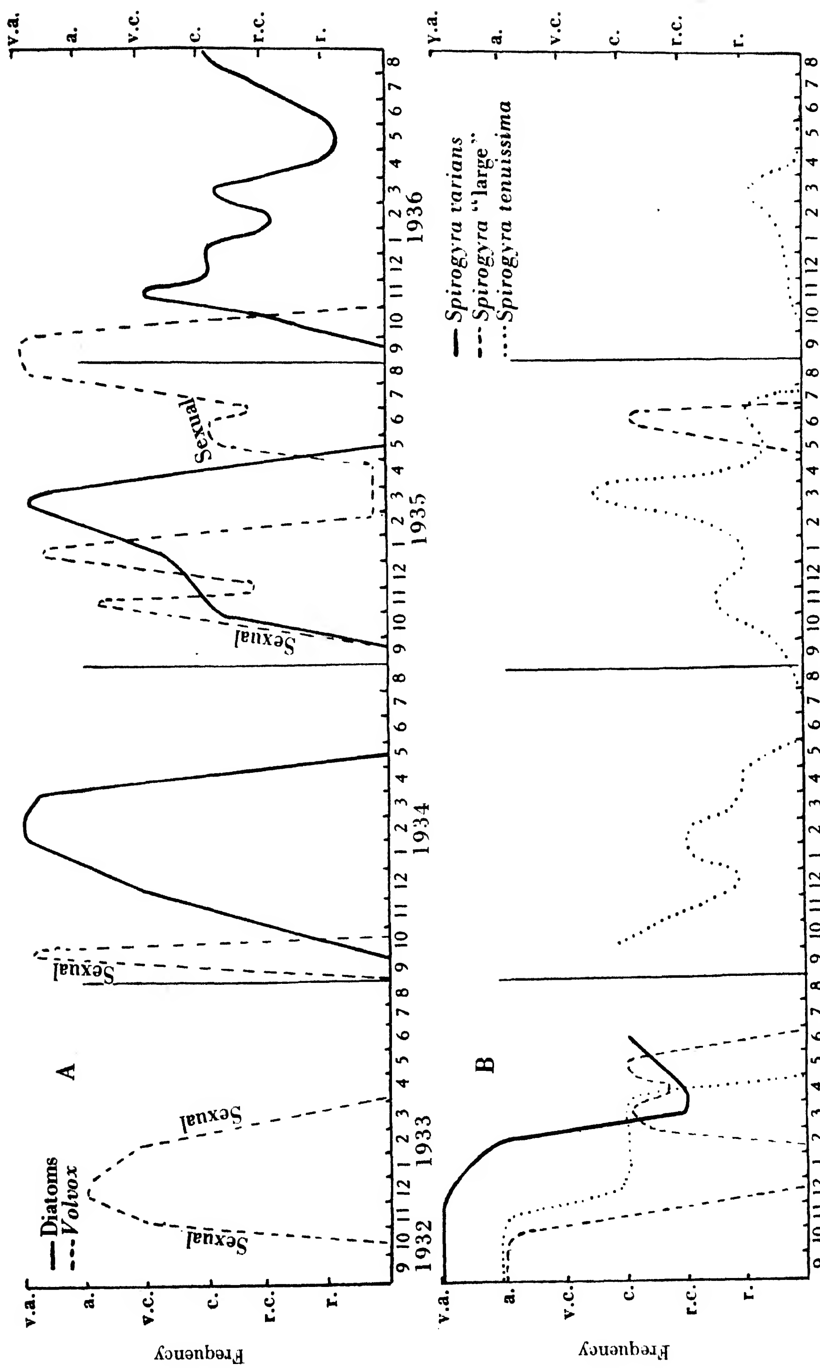

FIG. 4. Curves showing relative abundance of algae. A, *Volvox aureus* and diatoms; B, *Spirogyra* spp.

Beauchief the alga survived two periods of ice during relatively sunless winters and was often absent during the sunniest months of the year (Fig. 4A).

More important than weather conditions was the influence of nitrate. Each year the September maximum was suddenly interrupted at a time when heavy rains washed considerable nitrate into the pond (Fig. 2B). On visiting the pond a few days after the rains there was scarcely a colony to be found, whereas before, the water was coloured green by the alga. It is possible that many of the free-floating colonies were washed out of the pond, but it seems likely that enough would be left to give a fresh growth when conditions became favourable once more. Only in 1934 did *Volvox* regain its maximum after a severe check in November and in that year it was never completely absent. The fact that *Volvox* failed to reappear in the winter and spring of the other years may be due to the higher nitrate of the early months of these years (Fig. 2B). The absence of the late summer maximum in 1936 may be attributable to the same cause.

Periods of sexual reproduction are indicated in Fig. 4A and occur at times of low nitrate. Knoke (1924) found that much nitrate was harmful to *Volvox* grown in cultures and that low nitrate favoured sexual reproduction.

Conjugatae

Spirogyra. When the investigation was begun the pond was full of *Spirogyra.* Several species were present, but the conspicuous floating masses were mainly *S. varians* Kütz., while *S. tenuissima* Kütz. occurred around the *Elodea.* In the autumn and again in spring another large species made its appearance at the inlet end and spread gradually throughout the pond. From September 1932 to June 1933 *Spirogyra* was the most conspicuous alga in the three ponds and in the stream above and reached a maximum in December and January (Fig. 4B).

By September 1933 *S. varians* and the large species had disappeared and they have only been seen since as very occasional filaments during the summer months. It is possible that both species conjugated during the 6 weeks when the pond was not visited and if so it is surprising that the resulting zygospores have not given rise to a new generation. Another suggestion is that the high temperature and low water (Fig. 3A and B) of July and August 1933 had an adverse effect on the alga in the vegetative condition, possibly favouring the development of some parasitic fungus. Hodgetts (1922) and Fritsch & Rich (1913) both found an absence of the autumn phase following a period of low rainfall and plentiful sunshine.

Of the other species of *Spirogyra* occurring in the pond, only three were sufficiently common to be mentioned here.

S. tenuissima, though never very common, was hardly absent until, in common with other filamentous algae, it disappeared in the spring of 1936.

S. flavescens Kütz. occurred in the winter of 1933–4 and conjugated in

October. It was present again in the autumn of the following year, reached a maximum in March, and fell off till summer without being seen to conjugate.

S. affinis Kütz. was a spring form in 1934 and 1935, reaching a maximum and conjugating in June 1935.

The fact that these and other unidentified species were found shows that although the two original species did not reappear in quantity conditions were not unsuitable for the genus as a whole.

Mougeotia spp. Occasional filaments could be found mixed with other algae and round the *Elodea* at most times of year but never became common.

Desmidiaceae

Desmids were never a conspicuous feature of the pond. Species of *Closterium*, *Cosmarium* and *Staurastrum* were noted from time to time.

Cyanophyceae

Three genera were present at various times, *Oscillatoria*, *Anabaena* and *Nostoc*.

Oscillatoria curviceps Ag. reached a maximum in April and July but was seldom absent from some part of the pond (Fig. 5B). In the summer of 1934 the alga was plentiful in all parts of the pond but the maximum of other years was confined to the inflow end where occasional filaments could be found at all times in the mud. In November 1935 *Oscillatoria* was at a minimum in the lower ponds though the top pond was full of it and water was passing freely through. There was no appreciable difference in the nitrate, phosphate, or albuminoid ammonia of the three ponds at the time, and it is not yet clear why the alga failed to develop in the lower ponds. Hodgetts (1922) found that the *Oscillatoria* maximum coincided with a maximum concentration of dissolved salts. It may be significant that at all times when *Oscillatoria* was very plentiful the salt concentration was relatively high, and that the amount of dissolved salts was greater in the top pond than in the lower at the time when the alga was abundant in the former and absent in the latter. At other times of high salt concentration, however, *Oscillatoria* was absent.

Nostoc sp. appeared in August 1934 among the weed near the outlet. It never became common and was gone in October.

Anabaena constricta (Szafer) Geitler was common throughout the pond in October 1935 but all disappeared in the flood which followed. It appeared in small quantity each September and, like *Oscillatoria*, was more plentiful at the inlet end.

Oedogoniales

Oedogonium. Two species occurred. The smaller, *O. Braunii* Kütz., was usually attached to the *Elodea*, while the larger, *O. capilliforme* Kütz., was mixed with *Cladophora* and *Rhizoclonium* in free floating mats. Samples taken at all times throughout 1934 seldom failed to reveal occasional filaments of one

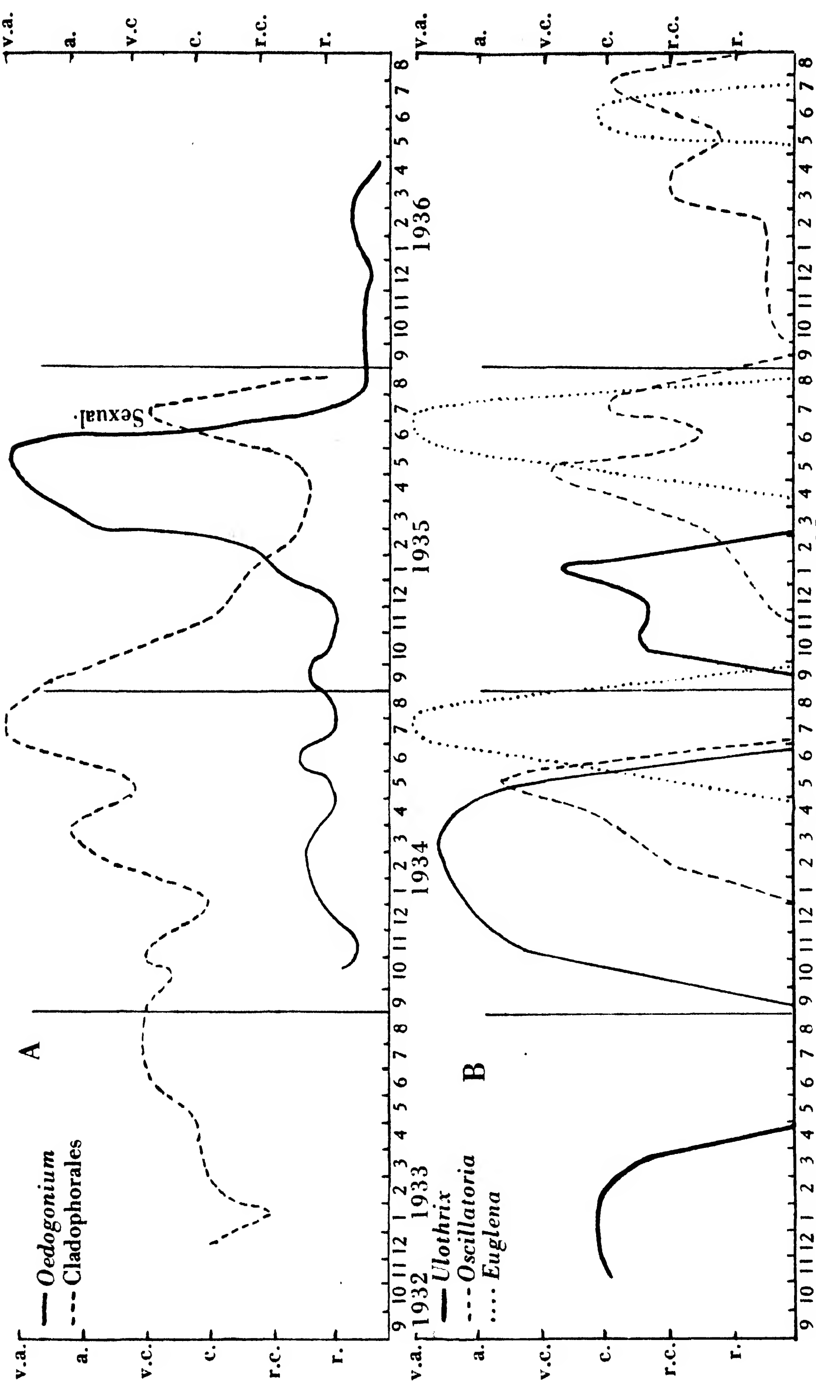

FIG. 5. Curves showing relative abundance of algae. A, *Oedogonium capilliforme* and Cladophorales; B, *Ulothrix tenerrima*, *Oscillatoria curviceps* and *Euglena sanguinea*.

or other of the species, but neither became common (Fig. 5A). In January 1935 *O. capilliforme* began to increase, became abundant in March, and in May and June formed dense mats over the whole pond. At the end of June it reproduced sexually and then rapidly died, its decay being accompanied by the appearance of an oily scum on the surface of the water. Since that time only occasional filaments have been seen.

There is evidence that *Oedogonium* does occur in "waves" of this nature but the reason for them is not yet clear. It has been suggested that the growth of the alga is favoured by sunshine (Fritsch & Rich, 1913) and that more prolific development follows high rainfall in the preceding months. While the maximum at Beauchief was reached at a time of abundant sunshine, an almost equally high record for the preceding summer did not appreciably affect the growth of *Oedogonium* (Fig. 5A). The rainfall in the early months of 1935 was greater than in 1934 (Fig. 3B); this may be a contributing factor.

Cladophorales

Rhizoclonium hieroglyphicum Kütz. and *Cladophora fracta* Kütz. formed dense mats at the surface of the water, particularly in the spring and summer of 1933 and 1934 (Fig. 5A). *Rhizoclonium* usually predominated and often there was a little *Oedogonium capilliforme* in addition. The curve showing the prevalence of these algae should be compared with that for *Oedogonium* (Fig. 5A). When the latter reached its maximum in 1935 *Rhizoclonium* and *Cladophora* were at a minimum. This suggests that there is competition between these larger mat-forming algae and that for some reason the early part of 1935 was favourable to the growth of *Oedogonium* which rapidly became predominant to the partial exclusion of the other two. When the *Oedogonium* died away there was a rapid increase in the quantity of *Rhizoclonium*. In common with most filamentous algae *Cladophora* and *Rhizoclonium* were rare or absent in 1936.

Ulotrichales

Ulothrix tenerrima Kütz. is a winter and spring form. From November 1932 to April 1933 it was common especially at the outlet end (Fig. 5B). It reappeared in October 1933, increasing rapidly till in the spring it formed dense mats on the *Elodea*. It declined early in June and has never become common since. In the 2 years just referred to the duration of the *Ulothrix* was approximately that of the nitrate (Fig. 2B). No spores of any kind were seen but fragmentation was common.

Ulothrix rorida (Thuret) formed a bright green growth from January to March on the stones over which the water tumbled as it overflowed from the pond. From January to about the middle of March zoospores were formed, but before the alga died off in April the filaments produced quantities of gametes.

Chaetophorales

Stigeoclonium sp. was found attached to the leaves of phanerogams from December to May each year but it never became common. It was also associated with *Ulothrix rorida* in the overflow stream.

Chaetophora tuberculosa (Ag.) occurred in May 1935 and April 1936 attached to grass near the outlet.

Coleochaete scutata Greb. was found on the *Elodea* leaves in spring and early summer.

Diatoms

In the first 2 years of the investigation, when the summers were dry, diatoms made their appearance in early October, increased to a maximum in March and had disappeared by the end of May. The chain forms became common earlier than those with single cells (Fig. 4A). This seemed at first to be a seasonal variation, the diatoms favouring colder weather, but when diatoms were numerous in the summer of 1936 (Fig. 4A) with a water temperature of 15° C. some other explanation became necessary. This was a very wet summer and the development of diatoms coincided with increased rainfall (Fig. 3B). Whereas in the two previous dry summers the nitrate content of the water was very low, in 1936 the figure was higher owing to the drainage water brought in after heavy rainfall (Fig. 2B). As the normal winter maximum of diatoms occurs when nitrate is relatively high it is reasonable to suggest that the increase of nitrate in the wet summer is at least in part responsible for the abundance of diatoms in 1936. Pearsall (1923) and Whipple & Parker (1912) have suggested that nitrate controls in some degree the development of diatoms in nature.

Figures for silica are only available for 1 year (App. 1) and are again related to rainfall. But the silica content of the water was always adequate and is unlikely to be a limiting factor in the growth of diatoms.

FLAGELLATA

A number of flagellates are given among the algae occurring in the pond, but few became abundant or showed a regular periodicity. The most interesting from this point of view was *Euglena*, which formed a regular part of the summer algal vegetation (Fig. 5B).

At the end of April 1934 a red scum made its appearance in the north-east corner of the pond and spread rapidly during the following months until in August it was continuous over the water and formed red rims round the algal mats. The actual scum was due to sheets of rounded resting cells and when the flagellates resumed activity they emerged leaving a film of brown cases on the water surface. At least three species of *Euglena* were present, the most

bundant being *E. sanguinea* Ehr. By the end of September the scum had disappeared.

The following year it came earlier in April, reached a maximum in July and had gone by the middle of August; and in 1936 it was present only near the inflow end for a short time in May, June and July. The groundsmen on the adjoining golf-course said that previous to 1934 they had never noticed the red scum.

After the disappearance of the *Euglena* in 1934, some mud from the bottom of the pond was brought into the laboratory and left in a glass tank in the greenhouse at a temperature of 18° C. In 2 days a greenish scum had appeared on the surface and proved to consist of resting cells of a red and a green species of *Euglena*. As the cells regained activity, the red colour which was concentrated in the centre spread throughout the cell. During the following weeks the alga increased until the tank was transferred to a ledge outside a window at 8° C. when the scum disappeared in 2 days. This suggests that the extent of the surface scum does not necessarily indicate the amount of the organism in the pond. Indeed, it was noticeable that on cool days very little was to be seen though the next warm, sunny day readily brought it back.

It is generally assumed that *Euglena* favours water with a high organic content. Fritsch & Rich (1913) found the maximum of *E. viridis* to coincide with a decrease in other algae which led to an enrichment of the water with organic matter. At Beauchief it will be seen that although *Euglena* was most abundant at times when albuminoid ammonia was at a maximum (Fig. 2 B) there was some other factor at work in addition. The highest figure reached for albuminoid ammonia was in August 1935 when *Oedogonium* was decaying, but at this time *Euglena* had already begun to decline. Probably the duration of the maximum is influenced by temperature.

SUMMARY

An account is given of the periodicity of certain algae in Beauchief pond during the years 1932–6 and of the changes in the physical and chemical condition of the water during that time. Records of sunshine and rainfall throughout the period are also given.

Nitrate. *Ulothrix*, diatoms, and *Spirogyra* react favourably to the presence of nitrate though in the case of *Spirogyra* the maximum of 1932–3 and its comparative absence in succeeding years must be attributed to some other cause. Two species of *Spirogyra* conjugated when nitrate was relatively low.

Cladophora, *Rhizoclonium*, *Oscillatoria*, *Oedogonium* and *Euglena* reached their maximum in the summer when nitrate was low. *Volvox* received a severe check when nitrate rose suddenly owing to the flood. It reproduced sexually at a time of low nitrate.

Albuminoid ammonia. This is at a maximum when nitrate is at a minimum, in late summer. *Cladophora*, *Rhizoclonium*, *Oscillatoria* and *Euglena* were

plentiful at this time. It would appear that these algae may be favoured by the presence in the water of the products of organic decomposition.

Phosphate. The fluctuations in phosphate are not closely related to algal periodicity. The supply was always adequate and the main variations occurred in the summer months following algal decay and at the time of frog spawning.

Sunshine has a direct effect in increasing the development of algae already present such as *Rhizoclonium* and *Oedogonium.* It must also be noted that, during rapid photosynthesis, these algae come to the surface in mats and are more noticeable than at other times. Sunshine may affect the growth of algae indirectly by raising the temperature of the water which also favours decay, and by changing the *p*H of the water through photosynthesis.

Rainfall. Heavy rain means an increase in the drainage water flowing into the pond, bringing with it soluble salts particularly nitrates and silicates. It has been shown that some of the algae are sensitive to the quantity of these substances in the water.

Germination of resting spores. The factors enumerated above combine in various ways to affect the growth and production of algae in the pond. But there is a further question which must be considered. Each summer there was a striking difference in the algae which composed the Chlorophycean maximum. *Spirogyra,* abundant in 1932 and 1933, was replaced in 1934 by *Rhizoclonium* and *Cladophora,* while in 1935 *Oedogonium* was the dominant alga.

In the summer of 1936, however, the pond was relatively sterile and no maximum of filamentous algae occurred. These algae used to collect on and around the *Elodea*, and the lack of this plant to form an anchorage may have been in some degree responsible for the dearth of algae. But in the mud at the bottom of the pond there must have collected resting spores of *Spirogyra* and *Oedogonium* in great quantity, and the question arises as to why they failed to germinate in the spring of 1936.

In order to find out whether there were in the mud any source from which these filamentous algae might spring under suitable conditions, some mud from the pond was brought into the laboratory in March 1937 and kept in covered jars in pond water. Filamentous algae soon appeared in the jars and up to the time of writing the following species formerly present in the pond have been identified: *Spirogyra varians, S. tenuissima, S. affinis, S. "large"*, *Oedogonium capilliforme, O. Braunii* Kütz., *Tribonema bombycinum, Euglena sanguinea.* It was particularly interesting to find *Spirogyra varians* and the large species of *Spirogyra* again, as only occasional filaments of the former had been seen in the pond since 1933 and the latter, which was abundant in all parts in 1933, had only appeared once since and in a restricted locality.

It is to be expected that these algae may again become abundant in the pond when conditions are suitable for the germination of their resting spores. What these conditions are may become apparent as observations on the pond continue.

Competition. There is no doubt that competition plays an important part in determining the composition of the summer maximum. Those algae for whose growth and development conditions are favourable in the early summer rapidly become dominant to the partial exclusion of other forms.

Variation in phanerogam population. Elodea canadensis, which covered the bottom of the pond at the commencement of the investigation, began to decrease early in 1935 and only a few patches were left by the summer of 1936. *Lemma minor* was abundant all over the surface from June to August 1934, falling off gradually until the end of October. It was present, but less abundant, in 1935 and in 1936 it appeared only round the edge of the pond. *Potamogeton natans* was equally plentiful each year in the places indicated on the plan (Fig. 1).

NOTES ON ANIMAL LIFE IN THE POND

Animal life was most abundant from January to November 1935, a period during which algae were also plentiful. The commonest forms were Ephemerids and Crustacea such as Daphnia, Copepods and Ostracods. They were less abundant in 1934 and very few were noticed in 1936.

In May 1936 and May and June 1935 Rotifers with eggs suddenly became very plentiful and then quickly disappeared. Snails were numerous on the water weeds from March to June 1935 and 1936 and a few were seen in November 1935. Their eggs were found in quantity on the weed in May. Frogs spawned each year about 20 March.

In conclusion, I wish to express my thanks to Prof. B. H. Bentley for the facilities he has offered me for carrying out these observations, to Mr J. G. Boswell for his help with chemical problems and to Dr W. H. Pearsall for his kindly help and criticism.

APPENDIX I

Amounts of dissolved substances in mg. per l.

	Nitrate N			Phosphate P_2O_5		
	1933–4	1934–5	1935–6	1933–4	1934–5	1935–6
Sept.	0·15	Trace	Trace	0·031	0·040	0·150
Oct.	2·40	Trace	0·80	0·022	0·039	0·029
Nov.	1·75	1·15	1·85	0·018	0·036	0·026
Dec.	1·97	2·50	2·30	0·027	0·023	0·035
Jan.	2·30	2·41	1·56	0·014	0·033	0·032
Feb.	1·58	1·90	1·82	0·015	0·033	0·029
Mar.	1·55	1·80	1·60	0·027	0·029	0·023
Apr.	1·55	1·40	1·27	0·040	0·050	0·006
May	0·51	0·24	0·25	0·054	0·039	0·012
June	0·13	0·13	0·71	0·079	0·063	0·011
July	0·10	Trace	1·02	0·090	0·199	0·174
Aug.	Trace	Trace	0·42	0·100	0·253	0·307

	Albuminoid ammonia NH_3 1933–4	1934–5	1935–6	Silica SiO_2 1935–6	Oxygen* 1935–6
Sept.	0·30	0·54	0·69	—	2·00
Oct.	0·33	0·52	0·30	4·63	1·50
Nov.	0·366	0·28	0·13	4·75	2·20
Dec.	0·16	0·21	0·17	5·00	1·25
Jan.	0·12	0·17	0·14	5·55	2·55
Feb.	0·15	0·16	0·07	4·50	2·71
Mar.	0·15	0·25	0·098	4·50	2·51
Apr.	0·19	0·22	0·09	3·50	2·56
May	0·24	0·23	0·28	3·00	2·22
June	0·45	0·50	0·16	6·00	2·37
July	0·45	0·66	0·29	7·15	2·14
Aug.	0·61	0·90	0·35	7·10	2·24

* Parts per 100,000.

Appendix II

Sunshine, rainfall and temperature

	Sunshine Daily average in hours 1933–4	1934–5	1935–6	Rainfall Monthly total in inches 1933–4	1934–5	1935–6
Sept.	4·72	4·70	4·70	1·620	1·779	4·145
Oct.	2·26	2·71	2·40	5·042	2·605	5·067
Nov.	1·36	1·06	1·70	1·829	1·972	5·814
Dec.	0·35	0·46	1·05	0·586	4·872	3·904
Jan.	1·53	1·50	1·06	2·709	1·500	3·230
Feb.	2·73	1·54	1·31	0·297	4·000	2·740
Mar.	2·43	3·10	1·34	3·039	1·539	2·080
Apr.	3·65	4·30	4·89	2·573	2·497	1·570
May	5·46	6·00	4·42	1·305	0·383	1·230
June	5·07	6·30	5·05	0·920	3·042	3·180
July	7·27	7·70	4·80	1·562	0·670	3·660
Aug.	5·14	6·20	5·08	1·084	1·997	1·270

	Water temperature Average of weekly readings in ° C. 1933–4	1934–5	1935–6
Sept.	12·50	22·0	12·5
Oct.	6·80	8·4	9·5
Nov.	5·60	6·0	6·5
Dec.	2·15	7·5	4·16
Jan.	3·15	6·4	3·5
Feb.	4·50	5·3	2·0
Mar.	5·25	6·6	6·6
Apr.	8·83	8·2	7·8
May	11·30	10·5	14·1
June	12·20	16·3	13·5
July	19·75	17·5	15·6
Aug.	21·50	17·0	16·0

APPENDIX III

Algae occurring in the pond but not mentioned in the text

[The numbers indicate months of the year.]

VOLVOCALES
- Gonium pectorale Mull. 5, 6, 7, 1934
- Pandorina morum (Mull.) Bory. 5, 6, 1934
- Chlamydomonas spp. 10, 11, 1933; 2–5, 1934; 5, 7, 11, 1935

CHLOROCOCCALES
- Pediastrum duplex Meyen. 4–8, 1935
- Scenedesmus denticulatus Lag. 3, 1936
- Scenedesmus obliquus (Turp.) Kutz. 4, 1936
- Scenedesmus quadricauda (Turp.) Breb. 4, 1936
- Scenedesmus spp. 4–6, 1935; 10, 1934
- Ankistrodesmus falcatus (Corda) Ralfs. 4, 1936
- Ankistrodesmus falcatus var. tumidus G. S. West. 4, 1936

ULOTRICHALES
- Microspora amoena f. minor Rabenh. 3, 6, 12, 1935
- Microspora floccosa Thur. 1, 1935

CHAETOPHORALES
- Aphanochaete repens A.Br. 5, 6, 1935 (on Oedogonium)

CONJUGALES
- Spirogyra spp.
- Closterium Leiblinii Kutz.
- Closterium Jenneri Ralfs.
- Closterium turgidum ? Ehr.
- Pleurotaenium Ehrenbergii (Breb.) De Bary
- Cosmarium spp.
- Staurastrum spp.

XANTHOPHYCEAE
- Tribonema bombycinum (Ag.) Derb. et Sol.

CHRYSOPHYCEAE
- Synura uvella Ehr. 3, 4, 5, 1934; 3–7, 1935
- Chrysococcus rufescens Klebs. 4, 1936
- Anthophysa vegetans (O.F.M.) Stein 12, 1933; 9–12, 1934; 9–11, 1935
- Mallomonas spp. 3, 1936
- Chromulina spp. 3, 1936
- Dinobryon sp. 5, 1936
- Chrysomonas sp. 10, 11, 1934; 9, 10, 1935; 2, 1936

BACILLARIOPHYCEAE
- Melosira varians Ag.
- Fragillaria capucina Desm.
- Meridion circulare Ag.
- Diatoma vulgare Bory.
- Licmophora flabellata Carm.
- Asterionella formosa Hass.
- Surirella robusta Ehr.
- Pinnularia viridis Ehr.
- Gomphonema constrictum Ehr.
- Synedra ulna Ehr. and other species
- Navicula spp.

This is only an incomplete list of diatoms in the pond.

CRYPTOPHYCEAE
- Chroomonas Nordstettii Hansgirg. 3, 1936

DINOPHYCEAE
- Gymnodinium aeruginosum Stein. 1, 1933; 5, 6, 1935

EUGLENINEAE
- Phacus triqueter (Ehr.) Duj. 3, 1936
- Phacus oscillans Klebs. 3, 1936
- Euglena acus Ehr.
- Euglena spirogyra Ehr.
- Euglena velata Klebs.
- Trachelomonas spp.

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NOTES ON THE ECOLOGICAL AND NATURAL HISTORY OF PABBAY, AND OTHER ISLANDS IN THE SOUND OF HARRIS, OUTER HEBRIDES

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(*With Plates II and III and two Maps in the Text*)

CONTENTS

1. Introduction: Pabbay

In the Sound of Harris, the channel between Lewis and North Uist, there is a cluster of small islands and rocky shoals. Pabbay, with its small neighbours the Shillays, a haunt of seals, lies some 4 miles out in the Atlantic. Beyond is only St Kilda, 40 miles to the west. Seen from the motor boat that carries one for an hour and a half from Rodel, in South Harris, between the islands of Killegray and Ensay, and past some seal-inhabited skerries, Pabbay appears as a broad-based triangular hill, with sand dunes covering the inner shore (Pl. II, phots. 1, 2).

From the top of this hill, which is called Beinn a' Chàrnain and rises to 644 ft., one can see a panorama of islands. In the Sound and just outside it are Lingay, Boreray, Spuir, Berneray, Coppay, Killegray, Ensay, the Saghays, and many others. To the south are the Haskeir Islands, breeding place of the grey seal. Far to the west is the St Kilda group, rising steeply from the Atlantic. Taransay lies to the north, not far from the Harris mainland.

It was with the idea of learning something about the mammals that I spent the week of 8–14 August 1935, camping on Pabbay, with the kind permission of the owner, Mr R. Campbell of Rodel, who also provided transport. I am grateful to all who gave me information; but especially to Messrs Donald

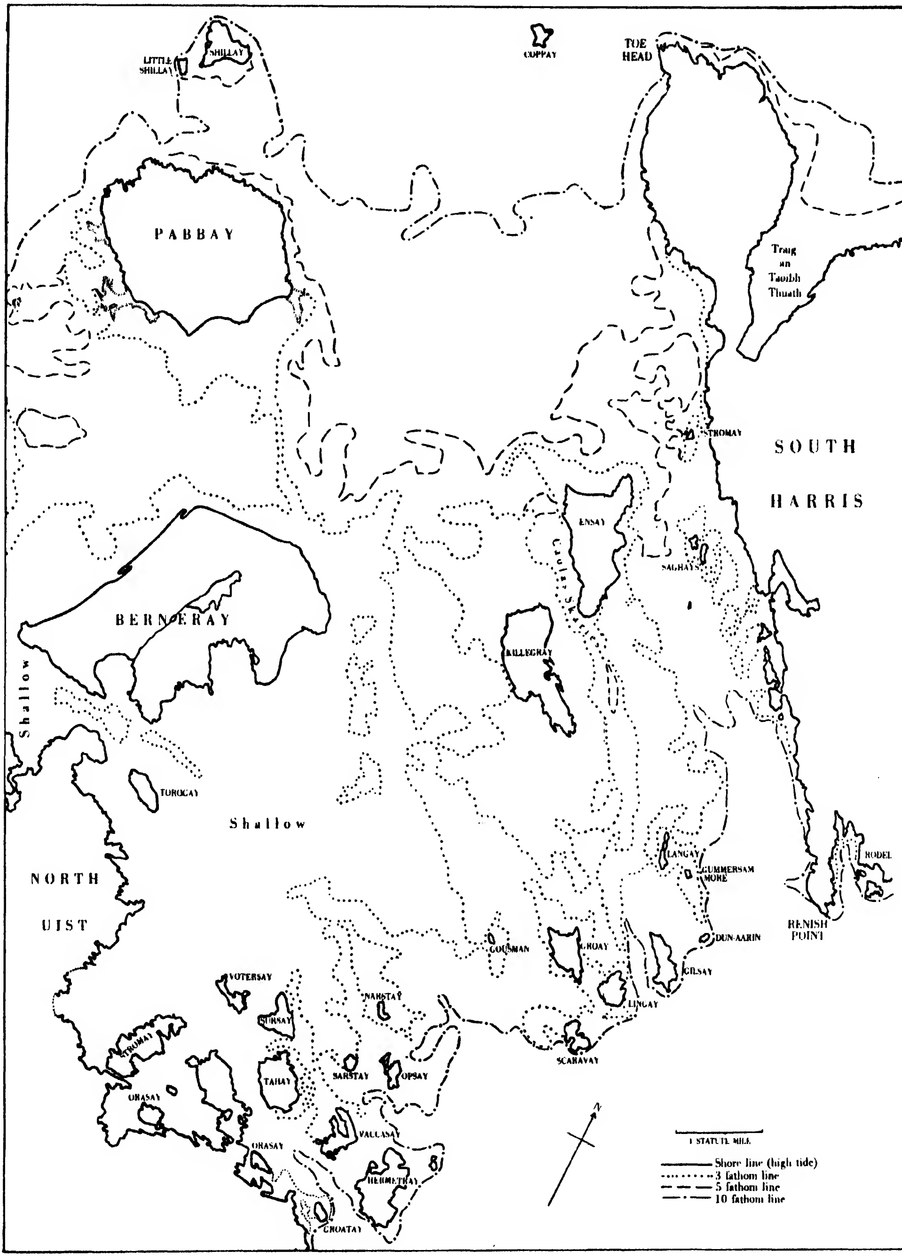

LITTLE SHILLAY
SHILLAY
COPPAY
TOE HEAD
PABBAY
Traig an Taoibh Thuath
STROMAY
SOUTH HARRIS
ENSAY
SAGHAYS
BERNERAY
KILLEGRAY
Shallow
TOROGAY
Shallow
NORTH UIST
LANGAY
GUMMERSAM MORE
RODEL
RENISH POINT
DUN-AARIN
GOUSMAN
VOTERSAY
NARSTAY
SURSAY
STROMAY
TAHAY
SARSTAY
OPSAY
ORASAY
VACCASAY
ORASAY
HERMETRAY
GROATAY
SCARAVAY
LINGAY
1 STATUTE MILE
Shore line (high tide)
3 fathom line
5 fathom line
10 fathom line

FIG. 1.

and Roderick MacDonald, the shepherds (and only human inhabitants) of Pabbay. They drew upon a deep island lore, and amongst other things told me where to catch pigmy shrews, where to find Martin's sunk forest and the remains of hazel in the island peat, and where the fulmars nest.

The survey was part of a wider plan of research carried out in co-operation with Mr D. F. W. Baden-Powell, the object of which is to reconstruct the Pleistocene and Holocene history of the Outer Hebrides and their fauna. To him, and to Mrs Jane Baden-Powell, I am grateful for much help in the preparation of this paper. Two papers on the parasites of mammals, and one on the fresh-water fauna, have already been published (Elton, 1934, 1936, 1937), also one on a kitchen-midden deposit (Baden-Powell & Elton, 1937).

Pabbay is made of solid rock, mostly hornblende-schist and gneiss of grey or black colour. In this are large dykes of white quartz and reddish rocks; and a line of flinty crush which continues across Shillay. The lines of these intrusions and pressures are parallel to the shores of Harris Sound. This rock is very near the surface in the central and northern parts of the island, and covered in many places with shallow peat. In the southern and western parts there is good pasturage, which turns on the inner, eastern slopes to pure sand dune, marram-covered. Apart from the shore line, some central small tarns, a few tiny streams, and the small oasis of cultivated croft, there are these three main ecological zones: heath, pasture, and dune—each with its swampy gradients to water, and salty gradients to shore.

Only two men live on Pabbay now; but some 90 years ago the population was much larger—over 200, on an island barely 2 miles across. The people were nearly all removed about the year 1842, it is said because of the whiskey which they distilled from barley grown there. I spoke with the one survivor from that prosperous time, Mr Donald MacLean of Northton in South Harris. At an age of about 89 his memory was extraordinarily clear and precise, and the story he told (Gaelic interpreted by his son-in-law, Mr Murdo Morrison) was this: Pabbay originally belonged to the MacLeods and then passed to the Dunmores, in whose time the exodus occurred, about 1842. Only six people stayed, including his father. He thought that some 200 people had been

FIG. 1. Map of Harris Sound, showing islands and main submarine contours. Data mainly from the Admiralty Chart, "Sound of Harris", which contains the surveys of Capt. H. C. Otter and others, published 1857 (large corrections 1865, smaller ones up to 1935). Soundings are in fathoms below low-water mark of spring tides. Thick shore line is high-tide mark. Owing to steep gradients on the lower part of the map, the five fathom line is omitted there; also in the deep channel, marked "Coalas Skaries", which runs mainly between the three and five fathom lines. Names follow the 1 in. Ordnance Survey maps. The map shows the complex clusters of small islands, the shallow col connecting Pabbay and Berneray, and the tortuous col running across the northern part of the Sound above the five fathom line. It is necessary to emphasize that these contours may not all apply to the present day, at any rate in detail, owing to the shifting nature of the sandy bottom.

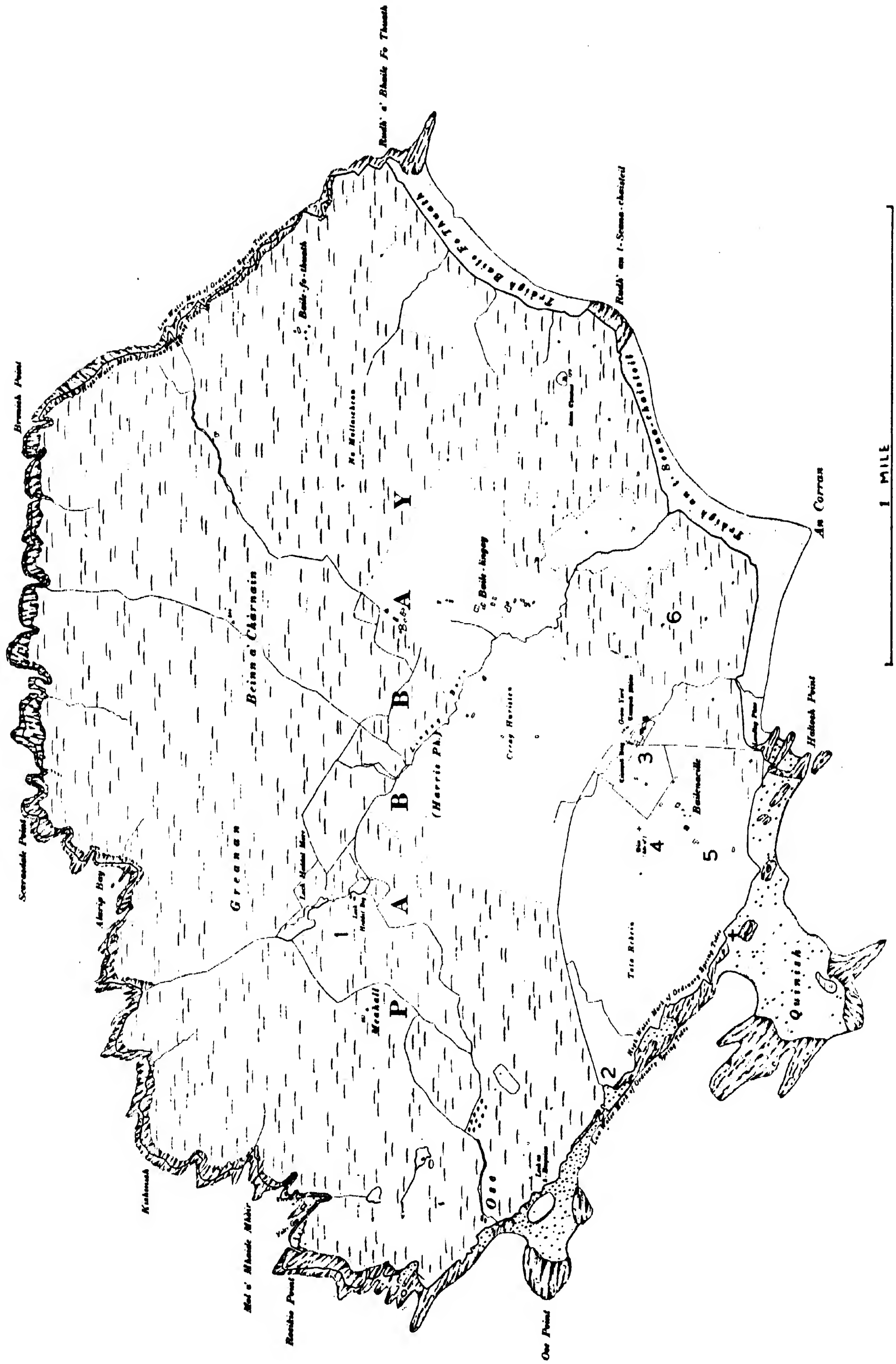


FIG. 2.

removed to the mainland, and that the population had been smaller than this at the beginning of the nineteenth century.

Groome's *Ordnance Gazetteer of Scotland* (1885) gives rather different figures for the population of Pabbay: in 1841, 338; in 1861, 21; in 1871, 8; in 1881, 2. These agree, however, in the main features of the exodus.

About 1863 the island was rented to the MacRaes, who brought in some new sheep from the mainland. Some rats got ashore from the boats, but for some reason they did not survive, and were found dead by the shore. This was the only time that rats ever came to the island. In 1865 the Dunmores sold Pabbay to the Stewarts of Ensay, who held it until four years ago when it was acquired by Mr Campbell. During the later period there were never more than six people on the island, chiefly managing the flocks for an absent owner. Now there are only two shepherds.

Pabbay is therefore one of the earliest Hebridean islands to have been depopulated, North Rona being the other one which was abandoned about the same time (1844). There are several other Pabbays in the Western Isles, not to be confused with this one. The name is not uncommon and means "Priest Island".

2. NOTES ON VEGETATION

These are general notes about some obvious distributions of the vegetation, with no pretension to deep analysis. They bear, however, on the ecology of the island mammals. Four things strike the eye. First, there are *no trees or shrubs* at all: an extreme form of the natural treelessness of the Outer Hebrides. As is later seen, birches and hazels at one time grew on Pabbay. Grazing, powerful winds, and little shelter, partly explain the present state. Another factor may have been the demand for fuel in this once heavily populated island.

The thinness of the *peat* is probably due to the same cause. There must at one time have been deeper peat than there is now. The scars of industrious cutting are still to be seen in the furrows that cover wide stretches of the rocky central part, on Meahall and Beinn a' Chàrnain. At present, peat deep enough for digging comes only in a few spots, as near Loch Heddal More, in the centre of Pabbay.

The two other striking influences are *sand drift* and *grazing*. These dominate much of the vegetation. The sand covers roughly the south-east quadrant of the island, partly as open dunes and partly as stable pasture. The cape of Rudh' a' Bhaile Fo Thuath marks one limit, except for some tiny patches of dune

FIG. 2. Map of Pabbay (O.S. 6 in. map, 1878, revised 1901, reduced, with following symbols added): 1. Site of hazel remains in peat; 2. Place where pigmy shrew was trapped; 3. Croft gardens, etc.; 4. Cairn (site of Dùn); 5. Walls, remains of ancient crofts; 6. Sand-dune trap-line (3–6 were areas on which mouse trapping was carried out); Cross, marking site of submerged trees and peat). (Reproduced from the Ordnance Survey Map, with the sanction of the Controller of H.M. Stationery Office.)

clinging to the eastern slopes. To the west of the landing place at Haltosh Point sand covers some largish patches near the coast, but never dominates the scene.

This sand invasion is not recent, nor do the dunes appear to be spreading inland at the present day. Sinclair in the *Statistical Account of Scotland* (1794, **10**, 344) made this note: "this island was once the granary of Harris, but it has lost much of its fertility by the encroachment of the sand drift, which now covers its S.E. side to the very top, exhibiting a most desolate appearance. The S.W. side is verdant and well cultivated. The N.W. side exposed to the Atlantic yields little or no vegetation, the spray of the sea in stormy weather washing over it." This would serve as a picture of the island at the present day, except that the poverty of the north-west side is exaggerated.

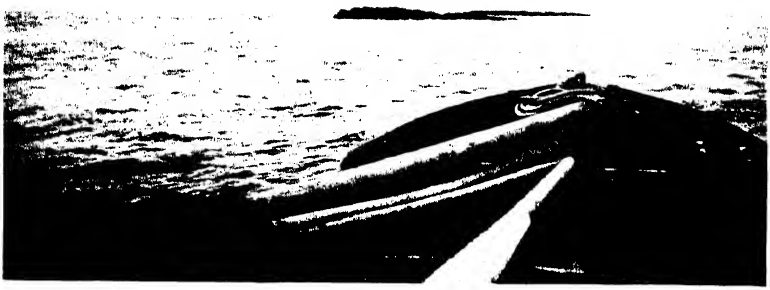
If Sinclair's account is accurate, we may conclude that the sand invasion occurred before the end of the eighteenth century. Several facts suggest that there was little or no advance in the nineteenth. For one thing, the ruined walls of the largest deserted village, Baile-Lingay, are high up on the sand-covered slopes, but have not been buried since 1842 by sand, nor has the smaller hamlet of Baile-fo-thuath. Again, Donald MacLean emphatically asserted that the dunes gave no trouble in the old days (i.e. the few years before 1842). Mr McGaskell of Rodel remembers that the seashore could be seen from the present croft when he was a boy, 40 years since. You cannot see it now, because the seaward dunes have grown in height. On the other hand, neither the croft, nor the ancient graveyard near it, have been overwhelmed by sand.

The explanation seems to be a stabilization of the higher inland slopes of sand-covered rock into a closed turf that is the favourite pasturage of the deer and sheep and cattle. These (in August at any rate) rather avoid the open dunes on the lower ground, also the relatively unpalatable thin heaths of the exposed northern rocks. It seems likely that the change from much arable farming to extensive grazing, lasting 90 years, has partly brought this stabilization about.

The tension zone between open dune and inland sandy pasture was examined at one spot near the croft. The last outposts of marram (*Psamma arenaria* Link)[1] give way rather abruptly to a low thick sward of well-cropped grasses: **Lolium perenne* L., **Cynosurus cristatus* L., **Holcus lanatus* L., **Poa trivialis* L., with a great deal of moss, **Hylocomium triquetrum* B. & S. The same four grasses were growing among the small marram plants on the tension zone. The vegetation is rather different on the old arable grounds, e.g. in one area there was also much creeping willow (**Salix repens* L.) also **Festuca ovina* L. (viviparous form).

The sheep, which seem to go about mainly in parties of nine to fifteen, in several places break down this closed vegetation by burrowing into the hill-side for shelter from the wind. These small hollows seem to have developed into quite large blow-outs in at least one gully below Baile-Lingay.

[1] Asterisks show that identification was backed by collected specimens.



Phot. 1. Pabbay (low conical hill) and Shillay (small lump in right distance), skerries (in centre foreground) seen from entrance to Harris Sound.

Phot. 2. Shillay and Little Shillay, seal islands off the north coast of Pabbay.

ELTON—Notes on the Ecological and Natural History of Pabbay

The rocky regions in the west, north and centre are mostly grown with poverty-stricken ling (*Calluna vulgaris* Hull.), much of it on rather wet ground. In some places there is a curious mixed assemblage, with *Calluna vulgaris*, *Erica tetralix* L., **Orchis ericetorum* Linton, **Sieglingia decumbens* Bernh., *Potentilla erecta* Hampe, *Primula vulgaris* Huds., *Narthecium ossifragum* Huds., *Euphrasia* sp., **Hypericum pulchrum* L., and *Anagallis tenella* Murr. *Empetrum* occurs very locally.

The combination of primroses, spotted orchids, ling, bog pimpernel, and bog asphodel seems unusual to anyone acquainted only with English vegetation. These grow on an exposed north slope open to the Atlantic, among wet rocks, not far from the sea-cliffs.

On the sandy machar by the landing place, relatively protected from sheep and not invested by marram, the grass and red clover (*Trifolium pratense* L.) is mixed with another set of flowers which includes frog orchids (**Coelo-glossum viride* Hartm.) and **Gentiana campestris* L., **Thalictrum arenarium* Butch. (a variety in the aggregate species *T. minus* L.) and **Antennaria dioica* L. The last is common in several habitats on the island.

In certain areas near the south-western shore there are large patches of almost pure silver-weed (*Potentilla Anserina* L.)

The remaining vegetation includes the dunes, dominated by marram (*Psamma arenaria*) which is extremely thick and luxuriant on the seaward edge; various damp and marshy communities, from which **Epilobium palustre* L. and **Comarum palustre* L. were collected; aquatic plants in the central tarns, including **Triglochin maritimum* L. *Molinia coerulea* Moench. occurs sparsely in various places, but never forms any impressive tussocks.

I owe the identification of the collected specimens (which are in Kew Herbarium) to Mr V. S. Summerhayes, Mr W. B. Turrill, and Mr C. V. B. Marquand, to all of whom I am grateful.

3. THE SUBMERGED FOREST

Pabbay was not always treeless. There are remains of woodland and scrub in peat deposits. This peat comes both above and below sea-level. The submerged forest here has been known for at least 230 years. It was first described by Martin Martin, a private gentleman with medical training who lived in Skye and voyaged among the islands. His most famous journey was to St Kilda in 1697, and it was possibly then that he collected notes on Pabbay; for he says (p. 123) that the Steward of St Kilda dwelt on Pabbay. This was one of the facts that influenced me to visit the island, as it seemed possible that the peculiar St Kilda mice might have been transported thither.

The other fact which decided me to go there was Martin's account of the submerged forest, which had never been studied: "The west end of this island, which looks to St Kilda, is called the wooden harbour, because the sands at low water discover several trees that have formerly grown there. Sir Norman

MacLeod told me that he had seen a tree out there, which was afterwards made into a harrow" (pp. 122–3).

Sinclair (1794, **10**, 373–4) also described this old forest: "Where the sea ebbs out in spring tides to a great distance, there are visible, at the very lowest ebb, large trunks of trees; the roots of which, spread out widely and variously, are fixed in black moss, which might be dug for peat to a great depth. Nor is this peculiar to Harris. The same, and other phenomena of the like kind, are observable along the whole sandy shore of the Long Island."

Although the St Kilda mice did not materialize, traces of the submerged forest were found on the shore side of Quinish isthmus. Several hours' work was done, so far as the tides would permit. The deposit is over 2½ ft. thick, the peat made chiefly of *seaweed*, hard packed, in which are remains of trees, apparently stumps *in situ*, with bits of branches also. This seaweed must gradually have replaced most of the original peat as this was washed away (Pl. III, phot. 3).

The bed is in several patches, covering altogether about 100 × 20 yd. Its situation is rather peculiar; west is a low ridge of intertidal rock, southward rocks rise above high tide, and south-east more rocks, sand-covered, and intertidal. This rock basin protects the deposit from full ocean force, forming a miniature harbour which no doubt explains why the forest has survived so long on this open coast.

Although no exact measurements were made, the surface of the peat was judged to be about 6 ft. below high-tide seaweed mark. The bottom could not be examined easily, since there was standing water below about 2½ ft.

The materials I collected were examined carefully by Mr M. Y. Orr of the Royal Botanic Garden, Edinburgh, where they are now deposited. I have to thank him, and the Regius Keeper, Sir W. W. Smith, for so kindly supplying reports that are drawn on here.

(1) Fragments of bark (up to 7 in. long) from the surface of the deposit are birch (*Betula alba* L.). In the accompanying peat are pollen grains of birch (*B. alba* —abundant), oak (*Quercus* sp.—1 grain), species of Caryophyllaceae and Compositae; tetrads of Ericaceae; and spores of *Polypodium vulgare* L. and *Sphagnum* (latter ab.).

(2) Embedded in seaweed peat at 1–1½ ft. were a trunk and small branches of *Betula alba*.

Other parts of this district have similar traces of ancient submerged peat and trees. Jehu & Craig (1927, p. 461) state that peat goes below high-water mark in some inlets in South Harris, and they instance Charnish (apparently Chaenish of the O.S. 6 in. map) on Killegray, in the Sound of Harris. Beveridge (1911, p. 6) writing of North Uist says: "Upon the northern shore of Vallay, in two small bays nearly a mile apart, the roots and branches of trees may usually still be found embedded within a layer of peat, disclosed here and there through the continually shifting sands. This feature is observable down to low-water

mark, and even slightly beyond that point, and certainly testifies to great changes both in climate and in the relative levels of land and sea." These two small bays are "Camas Mòr and Bàgh nan Craobagh or 'bay of small trees'. At this latter spot the writer has often seen trunks and branches lying in peat at a level about twelve feet below high-water mark. These measured up to a diameter of about fourteen inches, and apparently represent the birch. It is to be noted that elsewhere the island of Vallay now contains no peat, and is even practically without heather."..."At Kilpheder, on the Atlantic shore of North Uist, a solid layer of peat also shows under the stones on the beach near low-water mark." Sinclair (1794, **13**, 321) also mentions the Vallay forest.

F. MacRae, the minister of North Uist parish, writing in 1837 (published 1845) also mentions sunk forests, which "are found under high-water mark, nearly as low as the water recedes at spring tides, embedded in black soil or moss.... This is particularly the case, on no limited scale, near my residence" (the whereabouts of which he does not mention). He adds a most important fact as well: "From this circumstance, it may be inferred, that the land must have largely extended its bounds beyond its present limits. This is still less doubtful from the fact that, several miles from the shore, moss is taken up on the flakes of anchors, where, covered by the sea, it could never have grown."

This is perhaps the only record off the Outer Hebrides of extensive sunk peat like that on the Dogger Bank, where it is similarly dredged up by trawlers. If the distance of several miles is correct, the banks between the Monach Islands and the Haskeir Islands and North Uist may have formed part of this sunk land.

In 1937 Mrs Naomi Mitchison and members of her family made some enquiries and investigations on Vallay, the results of which she has kindly communicated to me. They ascertained that MacRae lived at Old Vallay House on Vallay, so that it may be safely assumed that he was referring to the banks off the west coast of the Outer Hebrides. They also searched for the submerged forests at Bàgh nan Craobagh and Camas Mòr. At Bàgh nan Craobagh "when we dug at low tide in sand about 10 ft. below high-tide mark, about 60 ft. down the beach, we found the sand mixed with black mud about 18 in. down.... Digging a few inches below high-tide mark there was a grey layer 40 in. down, not clearly marked." In another place drift-line debris was found covered by several inches of sand. Several people stated that until a few years ago (say fifteen years) bits of branches could still be seen there at low tide, but that there had been nothing lately. At Camas Mòr, nothing was found either. Here was a great deal of rotting seaweed, some of which was covered by layers of sand. This evidence shows that the remains of the submerged forest have either been washed away entirely, or are now covered up with sand.

This submerged peat on Vallay is referred to by Jehu & Craig (1926, p. 474), who state that "on the northern shore of the Isle of Vallay, in two bays not far apart, roots and branches of trees are found embedded in a layer of peat

exposed at times by the shifting of the overlying sands on the beach. This peat was observed to extend down to the low water and slightly beyond. The peat encloses fragments of birch and pine." They give a photograph of this peat, but as this was supplied by someone living on the island it is not certain at what date it was taken, and whether the peat was there in 1924. The same authors also mention submerged peat at some other points in this region of the Outer Hebrides. "Peat passing under high-water mark was observed at several other localities, as, for instance, near Creagorry (South Benbecula), in the south of Wiay [Benbecula], in the upper reaches of Loch Eport [North Uist], and at the south-west corner of Berneray [Harris Sound]." They also comment on the general "drowned" appearance of these coasts.

To the "woody" place-name noted by Beveridge, we may add one on Pabbay itself, Mol a' Mhaide Mhòir, which appears to mean "bay with large trees (or timber)". It is on the west coast, and about a mile north-west of the Quinish deposit I have described. Unless the name refers to driftwood, which is unlikely, there may be or may have been more forest at this point. The early accounts mention large trees at lowest tide: neither applies to the Quinish bed, though this is the only one now known to the MacDonalds. Again Martin says "the west end...which looks to St Kilda, is called the wooden harbour". This description fits either locality quite well.

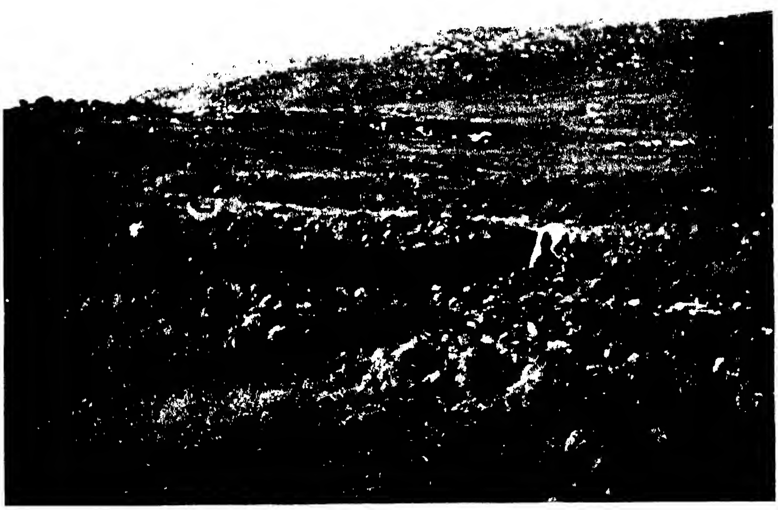
On the west coast of Boreray, about 5 miles from Quinish, is Rhudha Mhaide, which appears to mean "point with trees (or timber)", while the islet "Craobhagun", on the Harris Sound coast of North Uist, may have a similar significance.

Remains of scrub, not hitherto recorded, occur in a peat section near Loch Heddal More in the centre of Pabbay (Pl. III, phot. 4). This peat is used for fuel: it lies in a flattish marshy patch. The top 12 in. is formed of the present grassy turf. Below this for 8 in. thick fibrous peat passes down into black peat over gritty native rock. At the junction of turf and peat are blackened dead rhizomes of horsetail (*Equisetum limosum* L.)—which still grows in a nearby marsh—and fragments of the bark of hazel (*Corylus Avellana* L.).

The first sample of the peat examined by Mr Orr held "pollen grains of *Betula alba* (abundant), *Corylus Avellana*, *Pinus sylvestris* (occasional), species of Caryophyllaceae, Umbelliferae (*Oenanthe? Lachenalii* Gmel.), Cyperaceae and Gramineae; tetrads of Ericaceae; spores of *Equisetum*, *Polypodium vulgare*, and *Sphagnum* (ab.)".

Another sample consisted of a complete section through the 8 in. peat. Mr Orr reports as follows: "Samples of peat, taken from different parts of the section, were examined, and it was found that the composition of the pollen content was comparatively uniform throughout the section, although the amount of pollen present was greater, perhaps, near the upper surface and in the middle than at the gritty end.... Tree pollen was scarce, but there appeared to be little difference between the pollen-content of this section of peat and that

Phot. 3. The sunk forest on Pabbay is in the bed of peat about the centre of the photograph. Two other bits of peat are seen in the right foreground. High-tide mark (seaweed drift) in the background. Seaweed and sand elsewhere.



Phot. 4. The buried hazel wood remains lie near the base of this peat section, which is in the centre of Pabbay, near Loch Heddal More. Ancient croftland ridges and walls just beyond, and behind them Beinn a' Chàrnain with thin shaved peat on the rock.

of the samples previously examined from the same area. Pollen grains of *Betula alba*, *Corylus Avellana*, and *Pinus sylvestris* were found, the last-named being present in greater quantity in the middle of the block of peat than elsewhere. Pollen of members of the Caryophyllaceae, Cyperaceae, and Gramineae were observed, the grass pollen being the most abundant: tetrads of the Ericaceae were again very abundant, and pollen-grains of Composites (*Hieracium* or *Crepis*) occurred occasionally. The spores of *Polypodium vulgare*, and of another fern (*Aspidium* sp.?) were frequent, together with a few spores of *Lycopodium* and *Equisetum* sp....As before the spores of *Sphagnum* were particularly abundant throughout."

The absence of hazel pollen from the submerged forest, if confirmed by further work, suggests that the scrub was not contemporaneous with these birch woods.

It is well known that remains of trees and shrubs are abundant in the peat deposits of the Outer Hebrides, where, even on the larger islands, none but planted woods survive. Niven (1902) gives oak, pine, hazel, alder and birch from the Lewis peat. We have seen that birch and hazel once grew on Pabbay.

Similar woods occurred at Achmore (in the centre of Lewis, at about 300 ft.). Remains from near the base of a 3 ft. peat section were identified by Mr Orr as hazel bark (*Corylus Avellana*) and birch wood (*Betula alba*), together with rhizomes of horsetail (*Equisetum limosum*).

Other observations on the peat deposits of Lewis, made by Mr Baden-Powell and myself, are reserved for publication elsewhere. The whole question is of great importance in any discussion of the origin of the present fauna of the Outer Hebrides, which has a pronounced woodland character, especially in the birds and mammals.

There is some evidence that natural woodland lasted until historic times, and that it has only completely vanished in the last hundred years.

(1) Martin (1703; p. 92 in 1934 ed.) noted that "I saw big roots of trees at the head of Loch-Erisport [Erisort, on the East coast of Lewis], and there is about a hundred young birch and hazle trees on the south-west side of Loch-Stornvay [Stornoway], but there is no more wood in the island".

(2) Mr John Morrison, a well-known Stornoway naturalist, informed me that there used to be a few trees in the ravine near Stornoway Castle, before the present woods were planted there by the owner about a hundred years ago. This fact he had from one of the estate keepers.

(3) Sinclair gives nothing about this subject. But William MacGillivray, the famous Scottish naturalist, who spent his childhood in Harris and visited it frequently in later years, wrote (1830, p. 91): "In the island of Lewis, not far from the manse of Keose, there are the remains of a birch wood, the stunted bushes of which occupy a considerable extent of ground. I have seen a few trees of birch in the Forest of Harris about twenty feet high, and many poplars from six to fifteen feet high; but these were merely shoots from old roots which

remained in the crevices of rocks. *Pinus sylvestris* had formerly grown in the Forest of Harris, where some of its stumps still remain projecting through the moss, their roots being invariably in the subjacent clay or gravel."

Probably no naturalist has ever known Harris and Lewis as well as William MacGillivray, and his little-known account of the Outer Hebrides includes a survey of the vegetation on almost modern lines. He noted that dwarf trees of the following species grew along gullies and on islands: *Populus tremula*, *Betula alba*, *Corylus Avellana*, *Alnus glutinosa* and *Pyrus aucuparia*. These are undoubtedly much less common at the present day, with the exception of the rowan, which occurs on the lochan islets.

(4) The village manse of Keose lies on the north side of Loch Erisort (on the east coast of Lewis) not far from the mouth. Remains of a birchwood in this area are also mentioned in *The New Statistical Account of Scotland*, written by the ministers of various parishes about a hundred years ago. Cameron (written 1833, published 1841) says: "There is scarcely any wood in the island, except a few bark-bound birches in the parish of Lochs.... Out of Stornoway [in which parish he lived] there is scarcely anything like a tree seen, except for a few willows in gardens.... The greater part of the island seems to have been wooded in ancient times, as roots of trees are dug out of the moss; hazel nut shells are found, when the people cut their peats, at a depth of 14 ft. According to tradition, the Norwegians... set all the wood on fire, when they landed in the North Hebrides."

Much the same story was related to me in 1935 by Mr Murdo MacLeod of Bewglass, who said that it had been handed down from father to son, as a tradition. In this version, a Norwegian princess burned the pinewoods (that can be seen in the peat near Scaladale at the head of Loch Seaforth) in anger at a foreign prince who spoke admiringly of the Harris Woods, and not at all about her. The sagas certainly speak of the Outer Hebrides being swept by fire and sword when the Vikings came.

Finlayson (1841, written 1833) says: "There is a stinted scraggy copsewood of birch of small extent, in a point of this parish called Swordle, near the spot on which the first manse of this parish stood. This is the only wood now on the island.... Tradition says that the woods of Lewis were burnt by the Danes."

The O.S. 6 in. sheet (Island of Lewis Ross and Cromarty, 33, surveyed 1845–50, revised 1895–6) shows on the south side of Loch Leurbost a loch called Loch Coille Suardale, and by it a hill called Coille Suardale. This must be the place "Swordle" with the trees, since "Coille" is a wood in Gaelic. Since Finlayson lived in the parish of Lochs (including Lochs Erisort and Leurbost) he must have had the best knowledge, and it is likely that this surviving birchwood was not right at Keose, as suggested by MacGillivray, but near an earlier manse at Suardale.

The statement of W. MacRae (written 1833, published 1841) who lived in the

western parish of Barvas, that there was "not a vestige of wood, or tree, and scarcely of a shrub" although "roots and trunks of fir, oak, and hazel, with hazel-nuts, are frequently found embedded in a great depth of moss" confirms the general picture we have already.

(5) In the mouth of Loch Erisort, which is an arm of the sea, lie several islets marked on the O.S. 1 in. map (1928–9 revision) as "Barkin Isles". These are really the "Birken Isles". "About 7 miles southward [of Stornoway] there is a good harbour, called the Birkin Isles" (Martin, 1934 ed. p. 87). "Towards Birken Isles Loch or Loch Erisort" (Headrick, 1800, p. 5). "Loch Luerbost [which enters Loch Erisort near the mouth], like Loch Bernera, consists of a deep indentation sprinkled with islets.... Whatever claim the Birken Isles may once have had to their name, they must long since have lost it, since neither birch nor any tree except a few stunted plants of *Populus alba* is to be seen through the whole extent of Lewis" (MacCulloch, 1819, p. 174).

(6) "Birken" is the Norse for "birch", and since MacGillivray and the others recorded birch scrub still growing a few miles away on the mainland in 1830–3, we are justified in believing that birches probably grew there during the Norse occupation of Lewis. This lasted from about the ninth century to 1263, when the Norsemen were driven from Scotland.

There have been, it seems, one or more periods when woodland grew extensively on Lewis and Harris, and in parts of Harris Sound now submerged by the sea. Also hazel scrub was present on Pabbay. Some of the mainland woods survived until a few hundred years ago, at any rate birch and hazel. We cannot say when the maximum of this last woodland period was, nor when submergence happened. Two points about the submergence are, however, worth considering:

(1) The lowest recorded submerged woods in the Harris Sound region are at lowest tides, i.e. some 11–16 ft. below high-water mark. The highest (Pabbay) is about 6 ft. below high tide. Now Pabbay and most of the other islands near it lie inside a 30 ft. marine contour, while the deepest part of the centre of the Lewis-North Uist strait is 50 ft. or less. These depths are from the Admiralty Chart, which refers them to low-water mark of spring tides. The shifting sandy bottom of the Sound adds an unknown factor of erosion and deposition that makes any argument from present contours dangerous. But it seems quite possible that an elevation of 30–50 ft. might convert Harris Sound into a shallow strait such as those that separate the two Uists from Benbecula, and which run dry at low tides. The submerged woods are evidence of submergence of at least 16 ft., and almost certainly more.

(2) There is an interesting and deeply grounded tradition among the people of Pabbay and Berneray (told me personally by three different men) that in former times the two islands were only separated by a very narrow channel, so that people could shout across and be heard, or even throw things across. In this connexion may be mentioned Sinclair's statement (1794, **10**, 344) of

Berneray (i.e. the one in Harris Sound) that "its N.W. side is much damaged by the breaking of sand banks".

The Admiralty Chart (No. 2642, Hebrides, Sound of Harris, based on a survey in 1857, with minor corrections since) supports this tradition, in so far as there is a clearly defined submarine bank connecting Pabbay and Berneray, at depths of 12–20 ft. below low-water spring tides.

The tradition may possibly be based on a real submergence within historical times. This would agree with the other evidence that woodland survived into Norse and even modern times. It might, however, have been the remains of a much earlier forest. Also the submergence might equally have been at an earlier time. The matter could perhaps be decided by systematic pollen analysis of submerged peats in this area, and it would probably be practicable to get bottom borings done in shallow water below low-tide mark.

4. The mammals of Pabbay

Mice and shrews

"Tring" box traps, baited with cocoa-nut or cheese, were taken for collecting small mammals. Mr Morrison, the shepherd of Killegray who formerly lived many years on Pabbay, and the brothers MacDonald, told me that brown long-tailed mice with white bellies occurred on the island, and that small shrews were to be seen near Quinish. Morrison said that there were shrews on Quinish, and the MacDonalds that they occurred also on the rocky hill of Meahall, among the peat.

Trap lines were set out as follows (see Fig. 2):

Place	Date	No. of traps	Catch
Sheds and byre, with stone walls	8/9th	20	None
Marram-grass dunes, 550 yd. line from croft to shore	9/10th and 10/11th	48	None
Garden of croft, with stone walls, oats, potatoes, cabbages	9/10th	22	2 mice
	10/11th and 11/12th	22	None
Ruined walls of ancient crofts, and cairn, in pasture, Tota Robein	9/10th	25	2 mice
	10/11th	25	3 mice
	11/12th	25	2 mice
	12/13th and 13/14th	47	None
Stone walls and cairn by Loch Heddal More	11/12th	25	None
Rocks between Quinish and Ose Point, above tide-mark	12/13th	17	None
	13/14th	17	1 shrew

The two species described by the shepherds were caught: the Hebridean mouse (**Apodemus hebridensis* De Winton) and the pigmy shrew (**Sorex minutus* L.). Mice were scarce, only nine being caught in 410 trap-nights. Taking only the places where mice were caught at all, there were nine in 235 trap-nights. All the mice, and the shrew, were alive. The skins and skulls are in the Bureau of Animal Population, and are reserved for the Royal Scottish Museum, Edinburgh. The weights, measurements and breeding condition are given below. The weight of No. 7 does not include that of the embryos. Weights

are to the nearest gram. Lengths were measured to the anus. "Large testes" means about as large as those ordinarily found in breeding *Apodemus sylvaticus*. The proportion of males was very high in this small catch, while the proportion of young was notably meagre.

No.	Sex	Wt. g.	Body length cm.	Tail length cm.	Breeding condition
			Apodemus hebridensis		
1	♂	24	90	79	Large testes
2	♂	19	88	78	,,
3	♂	21	88	76	,,
4	♂	24	88	81	,,
5	♂	22	96	82	,,
6	♂	22	100	82	(Not noted)
7	♀	27	102	84	7 embryos (wt. 0·7 g.)
8	♂	24	100	84	Large testes
9	♀	11	78	67	Vulva imperfect
			Sorex minutus		
10	♂	3·5	60	44	?

The large size, coloration (the belly is very white), and the relative shortness of the tail stamp these mice as *hebridensis*. The tail is not only shorter than the body (instead of being equal or longer, as in the mainland species, *sylvaticus*) but its shortness increases relatively with age. It is well known that body measurements of dead mice are subject to errors due to the stage of relaxation after death. But this relative growth shows clearly also if tail lengths are plotted against weights.

A parasite survey produced six species on and in the mice, and one on the shrew. A report on these has already appeared (Elton, 1936). They were all species already known from *Apodemus sylvaticus* on the mainland.

No house-mice (*Mus musculus*) were seen or caught. It is possible that they occur, since in the Hebrides house-mice live on the croft lands in summer and are easily trapped. They go into the houses in winter. The shepherds trapped eleven mice in an outbuilding in the winter of 1934–5, and they told me that mice have been seen in the walls of the house and that one they caught was large and had a grey belly. If house-mice do exist, there are very few. Conditions for them are very unfavourable compared to what they were a hundred years ago.

Other rodents. There are no rabbits or rats on Pabbay. This is attested by all whom I asked who had lived there. The abortive colonization by rats in 1863 has already been mentioned. Voles (*Microtus*) are also absent. Having had considerable practice in hunting for vole traces, I can state this quite definitely. There are no runs in any of the dunes or grassland, and no traces of food or droppings.

Deer, sheep, and cattle. There is a large population of red deer (*Cervus elaphus*) which roam about the island in bands. They could be watched grazing indiscriminately among the sheep. These deer were introduced by the Stewarts

in the nineteenth century. Harvie-Brown & Buckley (1888, p. 34) note that "in 1886...we learned that some Red Deer had been successfully introduced quite lately to the island of Pabbay, Harris". They have been thinned out by the owner periodically; while McElfrish (1903) recorded that "a few years ago a number of deer left the island of Pabbay, swam across to North Uist and took up their quarters on the farm of Newton and the golf course at Trumisgarry". Apparently the North Uist deer refused to associate with the newcomers.

In 1935 the MacDonalds estimated the number of deer at 150. I saw at least fifty at one place; but the scattered, moving bands were hard to count, though easy for an expert shepherd.

As regards domestic animals, there were in 1935 500 sheep and forty-three cattle (besides a few ducks and hens). The sheep are dipped every year: I did not come across any ticks in the course of field-work. Every year the shepherds take sheep to market at Inverness. The cattle give very rich and excellent milk, which tasted to me faintly salt.

Land carnivores. There are two sheep dogs which stay with their masters, and two cats (not seen by me) which were ranging wild. The cats probably have an important effect on the numbers of mice. There are no indigenous carnivorous mammals.

Seals. These are numerous round the coast. The ones I saw were common seals (*Phoca vitulina*). They come round the Quinish rocks.

Conclusions. The land mammals of Pabbay are very few: the Hebridean mouse, pigmy shrew, possibly the house-mouse; and the introduced dog, cat, sheep, cattle and red deer. There are no rats, rabbits, voles, or indigenous carnivores. Many seals frequent the shores. The indigenous fauna (that is if we assume that the mice are not introduced) therefore resembles that of Lewis rather than that of North Uist; for voles (*Microtus*), which occur on North Uist, are absent from Lewis. This distribution is interesting, since Pabbay lies within the North Uist shelf, and within the 5 fathom line. The absence of rabbits is probably one reason for the richness of the grazing, for which several other rabbit-less islands of Harris Sound are famous.

William MacGillivray (1830, pp. 94–5) mentions the great fertility of these islands: "It would afford matter of astonishment to most persons residing in agricultural districts, to be informed that an island a mile in diameter, one-third of which is covered with sand, and at least a sixth bare rock, while the vegetation on the remaining part is never four inches high, should maintain two hundred black cattle, a hundred horses, and four or five hundred sheep, and yet this has been the case with the island of Pabbay, in the Sound of Harris." The total head of stock is close to that of the present day, if we include the deer (*c.* 750, *c.* 700).

5. THE MAMMALS OF OTHER ISLANDS IN HARRIS SOUND AND NEAR IT

I have not visited any of the islands except Pabbay, but was able to collect some notes from reliable people:

Shillay. Seals are very abundant, and Mr Campbell has seen them lying right up on the grass. Mr Fraser Darling tells me that this is usually the habit of the grey seal (*Halichoerus grypus*) rather than of the common seal (*Phoca vitulina*). The island has sheep on it, but no people.

Ensay. Mr D. McKenzie, who lived here at one time, said that the common brown hare (*Lepus europaeus*) had been introduced by the owner and was established.

Saghay Beg and Saghay More. He also told me that rabbits (*Oryctolagus cuniculus*) lived on one or both of these small islands in recent years. Sinclair (1794, **10**, 359) wrote nearly a hundred and fifty years ago, that "some of the uninhabited islands in the Sound of Harris abound with rabbits, introduced some years ago by the gentleman to whose farm these islands now belong". There are also sheep on the Saghays.

Killegray. This island, which is much covered with sand, supported 300 sheep in 1935. The shepherd, Mr Morrison, who had lived there for two years, said there are many rats (? *Rattus norvegicus*), but no mice or rabbits. He was well acquainted with the field mice of Pabbay.

Berneray. This is one of the larger islands, hilly at each end, and with sand dunes along the shores, especially on the outer sides. The large loch in the middle was said by Harvie-Brown & Buckley (1888, p. lvii) to be full of eels (*Anguilla vulgaris*). There is a large human population (something like a hundred families) on the island. Although rabbits (*Oryctolagus cuniculus*) occur, they are kept at low density by the large number of inhabitants. According to Mr Campbell they are almost extinct. There are rats and mice (D. MacD.). I showed an *Apodemus* to a visitor from Berneray, who said that long-tailed mice certainly occur there, but he was uncertain what kind: they do damage to stored crops in winter.

Taransay. Donald MacDonald knows this island, and he informed me that there are no deer, no rats, and no rabbits.

6. BIRDS

A few peculiarities of the bird fauna were noticed, although a proper account would have required a longer stay. Passerine birds were few both in species and individuals. The only ones seen inland were twites (*Carduelis flavirostris*), here taking the niche of sparrows around the croftland, and also seen by the shore; wheatears (*Oenanthe oenanthe*) on the hills; meadow pipits (*Anthus pratensis*) and rock pipits (*Anthus spinoletta*), both of which were also seen along the shore; and two ravens (*Corvus corax*). The MacDonalds stated that

wrens (*Troglodytes troglodytes*) have been seen, and that thrushes (*Turdus* sp.) occur in the spring months.

Three other birds are numerically important on the island in August, and presumably at a good many other times. Snipe (*Capella gallinago*) are extremely abundant in many parts of the island. Rock pigeons (*Columba livia*) also are commonly seen near the shore. John MacGillivray (1842), writing of the birds of Harris Sound, stated that the rock pigeon "breeds in great numbers in the maritime caves and fissures and nowhere more abundantly than in the island of Pabbay. During summer its food consists almost entirely of *Helix ericetorum* and *Bulimus acutus*, shells very abundant among the sandy pastures." The observation about the snails is apparently taken from the paper by William MacGillivray (1830, p. 325). The species are evidently the same as *Helicella itala* and *Cochlicella acuta*, mentioned in the next section as abundant on the dunes at the present day. Grey geese (probably grey lags, *Anser anser*) were often seen, especially on the grassy places around the central lochs of the island. In winter they are said to be extremely abundant. They may be of some importance in dispersal of fresh-water animals.

7. Lower life

Some general features struck one forcibly. No grasshoppers were seen, on dune, pasture or moor. It seems unlikely that this was due simply to a pause in the life cycle. Woodlice (including **Porcellio* and *Oniscus*) were extremely abundant under stones and in walls everywhere on the island. Snails were extremely abundant on the dunes, while bumble bees were conspicuous on the moor and sandy pastures. These two groups were studied a little.

On the dunes three snails were especially abundant: the large **Helix aspersa* Müll., grazing on white clover and other plants growing among the marram; the medium-sized flattish **Helicella itala* (L.) var. *instabilis* Jeffreys; and the long-pointed **Cochlicella acuta* (Müll.). Of the last, forty-eight specimens were collected at one spot in a few minutes. This species showed two colour phases (varying somewhat), and it was noticed that nine pairs, actually joined together, had mated dark to light, the other thirty snails being unpaired. The small **Trichea striolata* (C. Pfeiffer) also occurred on the dunes, while *Helix aspersa* was living in the garden, attacking cabbages.

Bumble bees of two species were rather common, visiting mainly the *Erica tetralix-Calluna* moor, and the red clover flowers in the sandy clover fields. Random collecting from flowers at several times gave: **Bombus s. smithianus* White, 22 ☿, 2 ♀, 3 ♂; **B. distinguendus* Mor., 3 ☿. Also at a sandy-stony-grassy spot near Ose Point there was on 13 August an assemblage of about twenty to thirty **B. s. smithianus*, apparently all males, since the thirteen collected were all of this sex. They were flying round near the ground, occasionally settling with vibrating wings.

Similar random collecting in four places at the same time of year in Lewis

in 1933 produced seventeen **Bombus s. smithianus*, seven **B. jonellus hebridensis* Wild, six **B. hortorum* L., eight **B. lucorum* L. *B. s. smithianus* was found at Barvas, Stornoway, and Scaladale in North Harris, *B. jonellus hebridensis* at Stornoway and Scaladale. It seems that *B. s. smithianus* is one of the commonest bumble bees in this region, and that the other three may be absent from Pabbay, where, however, *B. distinguendus* occurs.

Little attention was paid to other insects, but the following butterflies were recorded: white butterfly, *Pieris* sp. (caterpillars on cabbage); meadow brown **Maniola jurtina* Linn. (on pasture); the common blue **Polyommatus icarus* Rott. (on sand dune and pasture); also the ant, **Myrmica ruginodis* Nyl. In all places on Lewis and Harris where I have seen cabbages growing, the caterpillars of cabbage whites are a very serious pest (e.g. Dell, Barvas, Rodel, etc.).

The fresh-water fauna of Pabbay is very limited. The two shallow peaty tarns in the middle of the island, Lochs Heddal More and Heddal Beg, contain populations of small *Gammarus*, which also occur in the stream flowing down by Baile-Lingay. These differed in their habits from ordinary *G. pulex* in that they swam about freely in the open water in large numbers—a habit more often observed in *G. duebeni* in the laboratory. No specimens were taken. Dragonflies occur by the loch and Trichoptera in the streams. The grassy stream by the croft contained **Limnaea pereger* (Müll.) and **Planorbis spirorbis* (L.), the latter a new record for the Outer Hebrides.

These notes rest on identifications by the following, who kindly undertook the task: Dr O. W. Richards (*Bombus*: retained in his collection); Dr B. M. Hobby (Lepidoptera and ant: former damaged, not kept, latter in the Hope Department, Oxford); Mr G. C. Robson (land Mollusca: in the British Museum); Mr Charles Oldham (fresh-water Mollusca: in the Royal Scottish Museum).

8. MARINE LIFE

The West Coast of Scotland Pilot (1934) gives a description of Harris Sound: "The bottom is chiefly white shelly sand interspersed with rocks, which latter are invariably clothed with a reddish-brown seaweed of great length, and easily seen from aloft when the sun is high....Depths of 4 to $4\frac{1}{2}$ fathoms (7·3 to 7·8 m.) can be carried through the fairways of the principal channels...."

There is a long stretch of sandy shore running out below low-water mark on the south side. At the south-east point, Rudh' a' Bhaile Fo Thuath (which means Cape of the North Town), there is a great reef marked on the Admiralty chart. This runs out for a distance of half a mile and near the shore is densely covered with seaweed which can be seen floating at the surface.

Here on 11 August large flocks of sea birds were to be seen, including herring gulls (*Larus argentatus*), black-headed gulls (*L. ridibundus*), and eider ducks (*Somateria mollissima*), the latter with their families of young. On the shore rocks at this place were many rock pipits (*Anthus spinoletta*), and also starlings

(*Sturnus vulgaris*), and wheatears (*Oenanthe oenanthe*). Near here on the sand were many flocks of wading birds, including turnstones (*Arenaria interpres*), ringed plovers (*Charadrius hiaticula*), and dunlins (*Calidris alpina*). Oyster-catchers (*Haematopus ostralegus*), curlews (*Numenius arquata*), and ringed plovers are common round the shores of Pabbay. According to the MacDonalds, the fulmar (*Fulmarus glacialis*) has since 1929 or 1930 nested in Alarip Bay (Valarip Bay on the Admiralty Chart) on the north coast. In 1935 the number of pairs was estimated at about twenty.

On this long stretch of sand many shells had been thrown up and a collection was made, which has been examined by Mr D. F. W. Baden-Powell, who has kindly supplied me with the following list and some notes.

The following species of Mollusca were identified, and although only empty shells were collected, it is assumed that they belong to species living at present in the neighbourhood. The smaller forms (such as *Turtonia* and *Rissoa*) were obtained by sieving the sand which accompanied the specimens. The nomenclature is that of R. Winckworth's "British Marine Mollusca" (*J. Conch.* **19**, 1932); but some names used by J. Gwyn Jeffreys in his *British Conchology* (1862–9) are preferred or else added in brackets.

Modiolus modiolus (L.). Young
†Pecten maximus (L.)
†(*)Chlamys varia (L.)
†Cardium edule (L.)
†C. ?scabrum (Philippi). (C. nodosum). Young
†C. crassum (Gmelin). (C. norvegicum)
*Turtonia minuta (Fabricius)
Lucina borealis (L.). Young
†Venus ovata (Pennant)
†V. ?fasciata (da Costa)
†V. striatula (da Costa). (V. gallina)
†Dosinia exoleta (L.)
†Tapes pullastra (Montagu)
†T. pullastra var. oblonga (Jeffreys)
†Donax vittatus (da Costa)
†Tellina tenuis (da Costa)
†Spisula elliptica (Brown)
†S. subtruncata (da Costa)
†Mya truncata (L.)
†Thracia phaseolina (Lamarck). (T. papyracea)
†Solecurtus scopula (Turton). (S. candidus)
†Ensis siliqua (L.)
*Patella vulgata (L.)
*Helcion pellucida (L.)
Patina sp. Young
*Gibbula cineraria (L.)
*Calliostoma (Trochus) conuloides (Lamarck)
*Lacuna vincta (Montagu). (L. divaricata)
*L. pallidula (da Costa) ?var. neritoides (Gould)
*L. parva (da Costa). (L. puteolus)
*Littorina littorea (L.)
*L. littoralis (L.). (L. obtusata)
*Tricolia (Phasianella) pullus (L.) var. pictus (da Costa)
*Rissoa parva (da Costa) var. interrupta (Adams)
*Omalogyra atomus (Philippi)
Ianthina ?rotundata (Leach) (=I. britannica Forbes and Hanley)
*Trivia monacha (da Costa). (Cypraea europaea)
*Purpura lapillus (L.)
†Nassarius (Nassa) reticulatus (L.)

The species which normally inhabit sandy bottoms are marked with an obelisk (†), and those which live on rocks or seaweed with an asterisk (*). Several species, including *Lacuna vincta*, *L. parva*, *Rissoa parva*, *Omalogyra atomus*, and *Nassarius reticulatus*, also occur on *Zostera*, which grows on sand, although its presence in Harris Sound was not ascertained. These habitat notes are mainly taken from the remarkably good accounts given by Jeffreys (1862–9). The collection evidently contained a mixture of forms from the two main habitats (sand, and seaweed on rocks) described by the Admiralty *Pilot*.

The fact that the variety *interrupta* of *Rissoa parva* was found, and not the typical form, confirms Jeffreys' statement (1867, **4**, p. 25) that this variety is

more common than the typical form in north Britain; but the distribution of the two forms certainly overlaps to a large extent. The record of *Spisula subtruncata* at Pabbay may be of interest, as this species became extinct locally at Loch Gilp and Cumbrae, approximately between the years 1880 and 1905 (Stephen, 1935), although it was found at Tiree and Iona about 1903 (Knight, 1907), and in Shetland about 1860 (Jeffreys, 1862–9).

Stephen (1935), during his surveys of certain sheltered sandy shores on the coast of North Uist, noticed the scarcity or absence of *Tellina tenuis*, normally an abundant species in the lower tidal zones. He attributed this absence to the shallowness of the water over these sandy shores. The occurrence of *Tellina* on the shores of Pabbay suggests that conditions there may be more suitable for the development of a *Tellina* community.

The most interesting shell in this connexion is the *Ianthina*, which is probably *I. rotundata*; but this specific identification needs to be confirmed, as several species have been found. *Ianthina* is known to be carried by ocean currents for very great distances, and, according to Jeffreys (1867, **4**, p. 188), has even been known to reach our shores from the Straits of Magellan. The farthest north recorded for this form is Dunnet Head, in Caithness (according to Jeffreys, 1869, **5**, p. 214). It is very rarely found farther north than the south-west of Ireland. Its occurrence on Pabbay has already been published (Elton, 1936). Several other records of southern forms on the west coast of Scotland were noted in 1935.

There have been a good many records of tropical or subtropical species of marine animals drifting up to the west coast on the Gulf Stream. William MacGillivray (1830, p. 250) wrote that: "Several species of seeds from the West Indies, together with a few foreign shells, as *Janthina communis* and *Spirula Peronii*, are not unfrequent along the shores. Pumice and slag occur in small quantities."

The Admiralty surveyor, Otter (1867, p. 5), noted: "There is every reason to suppose that the Gulf Stream strikes upon the outer side of these islands and produces this high temperature. On the west shores of North and South Uist, seeds of West Indian plants, such as *Guilandina bonduc, Dolochosuzeus* and *Mimosa scandens*, as well as shells of the cocoa-nut, have been found, and go far in support of the above assertion, as does also the numerous wrecks in the same localities."

Beveridge (1911, p. 5) also comments on the fact that the air isotherms on the west coast of Scotland run north and south in winter, and attributes this to the Gulf Stream. He adds: "West Indian shells, beans, and seeds, together with cocoa-nuts (even in bunches), bamboos, and Sargasso weed from the Equatorial Sea, are (some of them frequently, others occasionally) cast ashore upon the west coast of North Uist, while the arrival of at least one turtle is chronicled about the year 1900." The "cocoa-nuts" of these accounts are evidently coco-nuts. The loggerhead turtle (*Thalassochelys caretta*) was found

in 1898 on the shore of Vallay, North Uist (Peel, 1899, 1901). It was a young one. Another, this time a female over 3 ft. long full of well-developed eggs, turned up at Dunvegan, Skye, in 1923 (Ritchie, 1924). These turtles are thought to originate from the Mediterranean region or from the West Indies.

Peel (1901) also mentions tropical seeds being washed ashore on North Uist. "Two very curious seeds were washed up and given me. One of these, a large red-brown one, flattened on the sides and measuring 5¾ inches in circumference, is known as *Entada scandens*, and is regarded as a charm in the Hebrides. The other—a smaller seed of a chestnut colour, surrounded by a lighter band in a black ring—is a species of mucuna, probably *Mucuna urens*, but although seeds of this and several other species are well known, they have not been satisfactorily connected with flowering specimens."

Mr MacDonald handed me a West Indian seed-pod measuring 5·1 by 5·9 cm., and dark brown in colour, picked up on the shore of Pabbay. Mr V. S. Summerhayes reports: "The seed is one of *Entada phaseoloides* (L.) Meu. (syn. *E. scandens* Benth. and *E. gigas* Fawcett and Rendle). This is the species which has been thrown up many times on the Hebrides, Orkneys, Norway, etc."

Further information on this subject, including some other records for the Outer Hebrides, can be found in Guppy (1917) and Colgan (1919).

9. Summary

In August 1935 an ecological reconnaissance was made of the small Isle of Pabbay, in the Sound of Harris, Outer Hebrides, with special reference to the mammals, and to evidence of former woodland on the island. Since the evacuation of the inhabitants about a hundred years ago, the island has reverted to pasture for a large number of sheep, cattle, and red deer (introduced about fifty years ago). The richness of the pasture is associated with the absence of rabbits. The small mammals are the Hebridean mouse (*Apodemus hebridensis*) and the pigmy shrew (*Sorex minutus*), which occur on the larger islands of the Outer Hebrides. Certain peculiarities in the rest of the fauna were noted. In the Sound of Harris there is a rich marine fauna, which forms the food of many seals and sea birds. Except for lobster fishing, there is little human fishing activity in this area. The submerged forest described by Martin in 1703 was examined and found to be birch (*Betula alba*). In the centre of the island there are remains of hazel (*Corylus Avellana*) under peat. Pollen from these peats was examined by Mr M. Y. Orr, who gives a report. There is much evidence of submerged woodland in the region of Harris Sound, also that some of the former birch and hazel woods on the mainland of Lewis survived into historical times. The markedly woodland aspect of the mammal fauna of these islands is interesting in this connexion.

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THE SOIL COMPLEX IN RELATION TO PLANT COMMUNITIES

III. MOORLANDS AND BOGS

By W. H. PEARSALL

While the preceding paper of this series dealt with woodland soils, this one describes in a similar manner some typical moorland soils, the primary basis of classification being the vegetation types occurring on them. The methods employed were described fully in the first paper of the series (1938). They determine the pH value from the potential at a bright platinum electrode in a quinhydrone saturated soil suspension, the determination being subject to the usual routine checks. Comber's thiocyanate test as modified by Misra is used to detect both base deficiency and the presence of replaceable ferrous iron. In the tables a single figure shows the depth of the colour with thiocyanate (scale 0–4). When a deepening of this colour is produced on adding hydrogen peroxide (one drop), the second colour is shown as a second figure, e.g. 2/3. The presence of nitrates in the fresh soil is detected by the production (in a clear aqueous extract) of a blue colour with diphenylamine. As nitrates are almost invariably absent in the soils described in this paper, only their *presence* is noted in the tables. The electrical potential of the soil is recorded in the tables as E_5, that is, the potential (E_h) in millivolts (mV.) corrected to pH 5 on the assumption that each unit increase of pH causes a decrease of E_h of 58 mV. The electrical potential thus measured is assumed to be an oxidation-reduction potential for reasons given in the first paper of the series. Further, because ferrous iron is usually present and nitrates are apparently not formed below an E_5 of 320 mV. soils of potential below this level are called *reducing*—while those above E_5 350 mV. are termed *oxidizing*. The latter contain no replaceable ferrous iron according to the test used. These previous conclusions are further exemplified by the data given in this paper.

The method of sampling chiefly used in this work has been to transport fresh samples of soil rapidly to the laboratory with as little disturbance of texture, aeration or temperature as is possible. As indicated in an earlier discussion, the toluol method of sterilizing is often less satisfactory with damp soils and hence has been used sparingly in the present series. A few results are also given for field determinations. Generally speaking, the aim has been to carry out the observations on unaltered soils. Normally the samples have been collected from a nominal depth of 10 cm. below the soil surface. On account of the irregularity of the surfaces, this depth must be approximate. Finally, the figures given represent late summer conditions (August and September). Almost all the soils described in this paper, with a few exceptions which are

duly noted, are, strictly speaking, peats. While the organic content of the samples here recorded has not been determined, previous estimates suggest that it is probably always over 85 % of the dry weight.

The samples thus taken represent soils beneath plant communities which are normally not subject to obvious biotic (grazing or human) influences and which are not undergoing rapid changes. The chief aim has been to describe soils of typical and extensive moorland communities such as heather or cotton-grass moors, and of necessity "raised bogs" ("hochmoor" or the "lowland moors" of English ecologists). A number of other conditions are included, most of which may be designated "mixed moors". For all of these a species list is given of the species present in a 1 m. quadrat round the sampling place. The attempt was made to choose sampling places typical of a wide area. Typical grasslands are not included.

HEATHER MOOR

Table I deals with the soil conditions where *Calluna vulgaris* was dominant, other species being usually infrequent. The first seven examples are all from extensive heather moors in Yorkshire or the Lake District. Many of the areas of this type in the Southern Lake District had originally much juniper present, and example No. 8 is representative of this state. The next two examples (Nos. 9 and 10) are from drained areas on raised bogs where *Calluna* had become completely dominant. All of these samples show remarkable similarity, with a pH value near to 3·5, and they are oxidizing soils (E_5 potential 400–500 mV.) which are markedly deficient in bases.

Table I

No.	Locality	Other frequent species	pH	E_5	Thio-cyanate	Remarks*
1	Blubberhouse, Y.	*Vaccinium Myrtillus* *Webera nutans*	3·41	527	3	265 m.
2	Blubberhouse, Y.	*Juncus squarrosus*	3·51	454	2	290 m.
3	Bingley, Y.	*Nardus stricta*	3·52	517	3	275 m.
4	Newby Head, Y.	*Hypnum cupressiforme*	3·61	445	2	400 m.
5	Coniston Moor	*H. cupressiforme* *Deschampsia flexuosa*	3·56	465	3	245 m.
6	Birker Moor	*Scirpus caespitosus* *Polytrichum commune*	3·47	460	2	260 m.
7	Kirkby Moor	—	3·49	471	3	230 m.
8	Yewbarrow	*Hypnum Schreberi* *Juniperus* adjacent	3·56	425	2	Juniper abundant, 245 m.
9	Birkett Close	*Hypnum Schreberi* *Vaccinium Myrtillus*	3·63	460	1	Drained bog
10	Ireland Moss	*Cladonia sylvatica*	3·55	440	2	Drained bog, 10 m.
11	Pillmoor, Y.	*Erica tetralix*	3·24	390	4	Sandy, 20 m.
12	Coupland	*Cladonia sylvatica*	3·69	510	3	Peat at 5 cm.
13	Coupland	*Hypnum Schreberi*	3·90	470	4	Sandy peat at 10 cm.
14	Hawkesworth, Y.	—	2·98	505	3	260 m., peat drained and burnt

Nitrates absent; Yorkshire localities shown by Y.

* Including altitude in m.

The last four examples, however, show points of difference. Nos. 11–13 represent samples from thin peats (i.e. from "heaths") overlying Keuper and Bunter sandstones. In neither case was the pure peat 10 cm. thick, and at this depth it was freely mixed with sand. For No. 12 (near Appleby in Westmorland), the peat at 5 cm. was also sampled. As was usually the case when this was done, the sample was both more acid and had a higher oxidation potential than the deeper sample. Sample 14 represents an anomalous condition. This was from an area which in 1922–4 was mainly covered by a mixture including both *Erica tetralix* and the cotton grasses, *Eriophorum vaginatum* and *E. angustifolium*. In 1936–7 none of these species was present. Frequent burning and a system of open drains had converted the area into one with *Calluna* dominant and, in fact, with remarkably little else. The low *p*H value of this sample should be noted. It is paralleled by the data given later for smaller patches of *Calluna* on redistributed cotton-grass peat (Table II, Nos. 24 and 39).

The interpretation adopted for these results is that *Calluna* moor in northern England possesses a very constant type of peat as judged by the available criteria. Two features of this peat type are of interest. It appears to be very similar to the woodland soils on which *Deschampsia flexuosa* is dominant and probably should be regarded as the unshaded equivalent of such soils. This similarity is of particular interest in view of the occurrence of *Calluna* moor on the sites of former forest and of the scarcity of tree seedlings in the *Deschampsia flexuosa* woodland community.

Secondly, the *Calluna* peats show no signs of marked deficiency in oxygen judging by their freedom from ferrous iron and their high oxidation potentials. In this also they resemble woodland "mors".

Cotton-grass moor

Cotton-grass moor is typically developed on gentle slopes of altitude above about 300 m. The peat is deep, commonly 2–3 m. and the vegetation almost confined to the two species of *Eriophorum* of which *E. vaginatum* is dominant. *E. angustifolium* is locally subdominant (usually in depressions) and constantly present. A marked feature of the typical areas is the extreme limitation of species and also very marked is the normal absence of *Sphagnum*. The peat is formed almost exclusively by *Eriophorum*. *Empetrum nigrum* and *Vaccinium Myrtillus* are usually abundant along the peat channels, the latter in what appear to be the driest places. *Empetrum* also occurs on redistributed peat and so does *Nardus stricta*. These species all form small pure communities.

The samples describing these moors are in series each collected at the same time from one locality. Each series starts with typical *Eriophorum vaginatum* moor, showing no signs of disturbance and then includes a series of local pure communities all on cotton-grass peat, with the possible exception of *Deschampsia flexuosa* on the adjacent steep slopes, but certainly on soil receiving the peat drainage.

Table II. *Cotton-grass moor* (*Yorkshire*)

No.	Locality and altitude	Species	pH	E_5	Thio-cyanate
15	Langsett, 400 m.	*Eriophorum vaginatum*, peat saturated	3·40	370	—
16		*E. angustifolium* d, *Sphagnum* f	4·35	360	—
17		*Nardus* = *Deschampsia flexuosa*	3·52	410	—
18	Wyke Head, 460 m.	*Eriophorum vaginatum*	3·20	225	1/2
19		*E. vaginatum* d, *Empetrum* f	3·02	275	1/2
20		*E. angustifolium*	3·03	330	2/3
21		*Vaccinium Myrtillus*	3·20	410	3
22		*Deschampsia flexuosa* d, *Galium saxatile* a	3·18	435	4
23	Wyke Head, 400 m.	*Eriophorum vaginatum*, caespitose	2·98	430	2
24		*Calluna* a, *Eriophorum vaginatum* o, retrogressive	3·15	450	3
25		*E. angustifolium* (redistributed peat)	2·94	405	3
26		*Nardus* d, *Juncus squarrosus* o (redistributed)	3·49	450	4
27	Buckstone Moss, 450 m.	*Eriophorum vaginatum*	3·31	360	2
28		*E. angustifolium*	3·44	320	1/2
29		Retrogressive *E. vaginatum* – *E. angustifolium*	3·16	415	2
30		*Empetrum nigrum* (peat redistributed)	3·28	475	2
31		*Nardus stricta* (redistributed peat)	3·35	510	3
32	Moss Moor, 440 m.	*Eriophorum vaginatum*, 5 cm.	3·29	390	2
33		As 30, 10 cm.	3·35	300	1/2
34		As 30, 15 cm.	3·38	220	1/2
35		*Nardus stricta*, sandy peat	3·30	570	4
36	Moss Moor, 400 m.	*Molinia coerulea*, oxidized peat	3·14	445	3
37		As 36, sandy peat	3·57	485	3
38	Moss Moor, 350 m.	As 36, turfy peat	3·73	455	1
39		*Calluna*, sandy, probably burnt	3·13	420	3
40	Standedge, 450 m.	*Eriophorum vaginatum*	3·24	335*t*	1/2
41		*E. vaginatum*, very wet	3·33	275*t*	1/2
42		*E. angustifolium* (depression)	3·05	235*t*	2/3
43		*E. vaginatum*, retrogressive	2·95	390*t*	2
44		*Empetrum nigrum*, near channel	2·82	390*t*	3
45		*Empetrum*, redistributed peat	3·31	420*t*	3
46		*Vaccinium Myrtillus*, channel edge	2·80	410*t*	3
47		*V. Myrtillus*, on peat hag	3·12	470*t*	3
48		*Nardus stricta* (redistributed peat)	3·30	460*t*	3
49		*Nardus* = *Deschampsia flexuosa*, on steep slope	3·54	400*t*	3

d, dominant; a, abundant; f, frequent; o, occasional; t, kept under toluol.

The typical *Eriophorum vaginatum* sample is a peat possessing a pH of about 3·3 ($\pm$0·1) and with a potential, E_5, of between 200 and 400 mV. The retrogressive areas, generally marked by strongly caespitose *E. vaginatum*, are normally more acid (*c.* pH 3·0) and more strongly oxidizing, the E_5 value being usually near or even above 400 mV. For example, Nos. 23–26 refer particularly to an area showing very marked retrogression and redistribution (owing to the cutting of a road).

E. angustifolium occurs abundantly on soils showing a far wider range of pH than *E. vaginatum*. (Note particularly Nos. 16, 20, 25, 42 and 99 and also the presence of *Sphagnum* in No. 16 with a pH value of 4·35.) The potentials recorded give E_5 values of much the same range as for the other cotton grass.

In the earlier papers of this series (1938) attention was drawn to the fact that an E_5 potential of 320–350 marked the limit below which reduction

processes predominated, by the criteria employed. The cotton-grass peats vary around this level, and at a depth of 10 cm. are often (in summer) slightly above it. They may be regarded as soils which are feebly oxidizing in summer. It should be clear that this property is confined chiefly to the superficial layers, and Nos. 32–34 in Table II show how the potential falls as the depth at which the sample is taken increases. At the same time the pH tends to increase. Hence if the usual potential at 10 cm. barely reaches the level at which soil oxidations predominate it is reasonable to assume that the main part of the peat (below 10 cm.) shows a potential indicative of reduction. Furthermore, the samples recorded are all for summer conditions, and for the dry season. The water level consistently approaches the soil surface in winter, and it will follow that then oxidation tends to be prevented, by lack of oxygen. Two points are emphasized, therefore, in regard to these peats. The bulk of the peat is *reducing* in character, though in summer at 10 cm. depth it reaches the potential level at which oxidation products can be inferred (three samples out of eleven). The superficial layers are, however, feebly oxidizing in summer.

In contrast to cotton grass, all the other species found on this type of peat occur where there is evidence of considerable oxidation—as E_5 potentials of 400 mV. and upwards. Particularly high potentials (up to 570 mV.) are recorded for localities on redistributed peat colonized by *Nardus*. This redistributed peat is normally black and amorphous, often mixed with sand (at 10 cm.) and it differs from the other localities sampled in tending to have a higher pH value than the adjacent undisplaced peat (see Nos. 26, 48). The latter is always marginal and partly oxidized as is shown by the higher E_5 potentials. Further these retrogressive and partly oxidized peats are the most acid soils encountered and there can be little doubt that the very high hydrogen-ion concentration is the result of the partial drying and oxidation of the original peat, because the two features are always associated.

The data given here are not adequate to distinguish between the habitats of the other species encountered, and indeed the sampling depth (10 cm.) bears no necessary relation to the rooting depths. Moss (1913) has drawn attention to the fact that such species as *Empetrum nigrum*, *Vaccinium Myrtillus* and *Calluna* have superficial rooting systems lacking the large internal air channels found in both species of *Eriophorum*. For this reason, Moss thought that the former species indicated partly drained soils no longer oxygen-deficient, a point of view in good agreement with the results recorded here.

Vaccinium edge

Another moorland type commonly recognized (see Moss, 1913) is the so-called *Vaccinium* edge or crest, developed on the steep edges of the escarpments or on occasional narrow ridges in the cotton-grass moor. *Vaccinium Myrtillus* is dominant, and usually *V. Vitis idaea* and *Deschampsia flexuosa* are present and often frequent. *Calluna* and *Empetrum* are local.

The soil status of this community is shown only by two examples from exposed moorland conditions. The samples were from Wyke Head (450 m.) and Blackstone Edge (500 m.), both rather sandy peats, with pH values of respectively 3·26 and 3·19, E_5 values of 415 and 440 mV. It will be noted that there is little difference between these on sandy and fairly shallow peat and the records for *Vaccinium* on cotton grass (Nos. 21, 46, 47) or raised bog peat (Nos. 98, 107) or the data previously recorded for woodlands (Paper II, Nos. 1–8, 86, 87). The soils are highly oxidizing, nitrates are absent and the pH value is normally below 3·4.

COMPARISON OF POTENTIAL DRIFTS

Another characteristic feature of the raw cotton-grass peat is that it shows comparatively small drifts in potential when taken into the laboratory. This is also a feature of many of the peats described later in the paper (e.g. those of raised bogs) and it is one which disappears in "oxidized" samples. Further, it is absent from *Calluna* moor peats which resemble the woodland "mors" described in the second paper of this series. We have no absolute method of estimating these drifts and so have to limit the comparison to samples which could be collected at about the same time and place. The various samples had a field temperature of 13–14° C. and large blocks were removed and kept at 20–21° C. in the laboratory. One sample (*b*) of cotton-grass peat was dug out loosely and repacked rather lightly, while sample *c* was treated similarly but then saturated with water. Samples *d* and *e* were from areas which had undergone denudation and oxidation. Sample *d* was from the edge of a peat "hag" and *e* was the blacker redistributed peat below this.

Changes in potential (E_5) in mV. in 48 hr.

	Vegetation	Treatment	Initial E_5	Change in E_5	Final pH
(*a*)	*Eriophorum vaginatum*	—	275	+ 12	3·23
(*b*)	,, ,,	Lightly packed	280	+ 35	3·26
(*c*)	,, ,,	Waterlogged	275	− 15	3·24
(*d*)	*Vaccinium Myrtillus*	—	435	+ 90	3·14
(*e*)	*Nardus stricta*	—	440	+170	3·46
(*f*)	*Calluna moor*	—	430	+120	3·53

It will be observed from these results that the unchanged *Eriophorum vaginatum* peats show comparatively small drifts, while the remaining samples, all of which from their situations must have undergone some oxidation, show larger drifts which tend to increase with the apparent increase in the amount of oxidation. The results in this table can be compared with those given in Paper II of the series for woodland soils.

It is of course possible that the close texture of these raw peats is partly responsible for the slowness with which the potential changes, especially if the peats are compared with woodland soils. But it is not easy to generalize about

this and in the examples quoted above the *Nardus* peat as collected was apparently wetter and closer than either *Vaccinium* or *Calluna* peat.

This matter is not, however, pursued further because the whole question of comparing the changes in soils by these methods requires more detailed attention and lies rather outside the scope of the present survey. It is simply recorded that a tendency towards rapid change of potential seems to distinguish the peats of *Calluna* moor and *Vaccinium* edge from those of the cotton-grass moors and raised bogs.

Mixed moorlands and bogs

The remaining moorland communities for which data are available usually lack any single dominant and normally include several frequent and widely distributed species. The records available were analysed by arranging them in order of *p*H. This is inconvenient for purposes of discussion although a very useful exercise as it suggests strongly that almost all these records belong to a single series in which Sphagna are normally present. No hard and fast line of distinction can be made in this series between what are undoubtedly "moors" (in the general sense of the term) and what must be termed "bogs". For convenience, the data are considered under the headings (1) Upland moors and bogs; (2) Connemara blanket bogs; (3) Lacustrine bogs; (4) Raised bogs.

(1) The upland moors, other than those falling into the categories already considered, are described in Table III, where the records are arranged in order of decreasing *p*H value. On this arrangement they clearly fall into groups, in the first of which, Nos. 51 and 52 represent "flushes" in moorland hollows. Both of these soils were peculiar in containing nitrates—carried down by drainage from adjacent grassland slopes. *Molinia coerulea* is usually abundant in these habitats and usually also *Myrica Gale* is present. These species tend to continue in the second group (Nos. 55–58) although they are less abundant. *Erica tetralix* and *Narthecium ossifragum* also are usually present. *Calluna* although frequent up to *p*H 4·7 (No. 53) is, in these records, only really abundant below *p*H 4·2.

The chief transition in this series of results comes about *p*H 3·8–4·0. Below this point, *Molinia* and *Myrica* are absent, *Sphagnum* is less abundant and *Eriophorum vaginatum* becomes prominent. It is noticeable also that while the soils are reducing in character above this *p*H value, below it they tend to be on the border line (E_5, 320–350 mV.) and about half of them are feebly oxidizing.

Further work on this group of soils is required. It is not known whether it is always the case that the soils from higher altitudes always fall in the third group and vice versa. Nor is it certain that *Empetrum nigrum* always alternates with *Erica tetralix* as in these records. It does seem to be the case, however, that the presence of *Eriophorum vaginatum* (and possibly *Empetrum*) indicates more acid and more oxidizing conditions (at a depth of 10 cm.) while the group *Myrica, Molinia* and *Narthecium* (with *Sphagnum* and *Erica tetralix*) is

on the whole characteristic of reducing and less markedly acid soils. The associates of this type of *Molinia-Myrica* community are emphasized.

Table III

No.	Place	pH	E_5	Thio-cyanate	Alti-tude	Additional species
		I. *Molinia coerulea*, f–a; *Sphagnum*, f–a; *Erica tetralix*, o–f				
51	Coniston Moor	4·98	260	2/3	220	*A, C, My, N*, Nitrates present
52	Birker Moor	4·80	270	3/4	240	*A, My, N, S*, Nitrates present
53	Maam Cross	4·66	—	1/3	50–70	*C, Cp, N, R, Schoenus*, a
54	Maam Cross	4·41	—	2/3	70–100	*A, C, N, R, Schoenus*
		II. *Sphagnum* and *Calluna*, f–a				
55	Blawith Fell	4·18	230	2/3	200	*M, N, O, S*
56	Birker Moor	4·11	280	2/3	260	*Cp, E, My, N, O, T*, a
57	Grass Garth	4·09	270	2/3	130	*M, N, S, T*
58	Coniston Moor	4·06	370	2	220	*A, Cp, J, M, T*
		III. *Calluna* and *Eriophorum vaginatum*, f–a; *Sphagnum*, o–f				
59	Wharf Head, Y.	3·78	412	2	570	*A, V, Empetrum*, f
60	Bowes Moor, Y.	3·77	275	1/2	480	*A, O, Empetrum*, f
61	Wharf Head, Y.	3·75	385	3	560	*N, O, T*
62	Newby Head, Y.	3·60	325	2/3	460	*A, O, T*
63	Swarth Fell	3·53	335	1/2	510	*A, J, T*
64	Bowes Moor, Y.	3·52	270	—	480	*A, T*, a
65	Bowes Moor, Y.	3·50	342	—	460	*Empetrum*, a
66	Newby Head, Y.	3·48	390	3	460	*A, S, T*
67	Ilkley Moor, Y.	3·47	300	2/3	320	*A, O, Empetrum*, a

Symbols used: *A*, *Eriophorum angustifolium*; *C*, *Calluna vulgaris*; *Cp*, *Carex panicea*; *E*, *Eriophorum vaginatum*; *J*, *Juncus squarrosus*; *M*, *Molinia coerulea*; *My*, *Myrica Gale*; *N*, *Narthecium ossifragum*; *O*, *Oxycoccus quadripetala*; *R*, *Rhynchospora alba*; *S*, *Scirpus caespitosus*; *T*, *Erica tetralix*; *V*, *Vaccinium Myrtillus*.

Frequencies: a, abundant; f, frequent; o, occasional. Places in Yorkshire shown by Y., others in English Lake District except Maam Cross in Connemara.

(2) *Connemara blanket bog.* Two samples, Nos. 53 and 54, in Table III (and No. 77 in Table IV) are representative of the conditions in the blanket bog of Connemara—the samples being taken on the hills south of Maam Cross. It is, perhaps, well known that these bogs, which clothe almost the whole country, contain *Molinia coerulea*, *Schoenus nigricans* and *Rhynchospora alba* as the most prominent species (see Praeger, 1934; Tansley, 1911). The description of this community used here is based on fifteen 1 sq. m. quadrats, of which five were taken on peaty flats near the numerous lakelets, five on slopes of average pitch and five on the steeper and better drained areas. Two soil samples of each type were taken, six in all. The thiocyanate test was done in the field and all the soils were apparently reducing and contained ferrous iron, although the reaction for this was faint in the soils from the steeper slopes. Samples were taken to England for pH determinations—some under toluol. The oxidation-reduction potential determinations were done after three days and again after keeping the soils at 13° C. for an extra three days. The potentials were always below E_5 300, and although the exact figures are probably not a reliable guide to field conditions, it is thought that all these soils are reducing. It would be inferred, as their appearance suggests, that they are usually waterlogged. Apart from the peculiarity of the presence of *Schoenus nigricans*,

the flora agrees fairly well with that of soils of similar pH in England (see Table IV particularly).

Table IV. *Soils of lacustrine origin* (*Lake District*)

No.	Locality	Additional species	pH	E_5	Thio-cyanate
		Carex inflata dominant			
68	Nor Moss	*Equisetum limosum, Menyanthes trifoliata*	5·88	220	0/1
69	Blelham	—	5·58	100	1/4
70	Birket Close	*Menyanthes*, a	5·47	150	0/2
71	Hawes Water	*Menyanthes, Equisetum limosum*	5·38	190	0/tr
72	Coniston Lake	—	5·38	165	1/3
73	High Cross	*Equisetum limosum*	5·35	240	0/2
		Sphagnum spp. with *Myrica Gale*			
74	Birket Close	*M*	5·59	110	0/2
75	High Cross	*A, D, R*	5·49	180	0/2
76	Blelham	*D, M, R*	5·46	190	1/3
77	Maam Cross	*A, D, M, R, T*	5·36	—	0/1
78	Low Water End	*A, D, M, N*	5·36	200	0/2
79	Birket Close	*A, N, T*	5·12	225	0/2
80	Low Water End	*A, D, M, N, R, T*	4·99	260	1/2
81	High Cross	*A, D*	4·96	200	0/2
82	Nor Moss	*M, N, T*	4·94	200	1/2
83	Low Water End	*A, M, N*	4·79	250	1/2
84	Nor Moss	*M, N, T*	4·60	310	2/3
85	Hawes Water	*C, M, N, S, T*	4·58	210	1/2
86	Birket Close	*M, N, T*	4·42	170	1/2
87	Birket Close	*A, C, N, S*	4·28	230	2/3
		Sphagnum with *Erica* and *Narthecium*, no *Myrica*			
88	Hawes Water	*C, N, T, S*	4·17	340	2
89	Hawes Water	*A, C, M, N, S, T*	3·94	300	2/3
90	Hawes Water	*A, M, N, T, S*	3·79	430	2
		Adjacent localities, drained, with *Molinia* dominant			
91	Hawes Water	*C, Betula* seedlings abundant	3·70	500	3
92	Nor Moss	*Betula* seedlings	3·66	430	1

Symbols used: *A, Eriophorum angustifolium*; *C, Calluna vulgaris*; *D, Drosera* spp.; *M, Molinia coerulea*; *N, Narthecium ossifragum*; *R, Rhynchospora alba*; *S, Scirpus caespitosus*; *T, Erica tetralix*.

A list of the species present is given in the Appendix. *Molinia, Schoenus, Sphagnum, Erica tetralix* and *Rhynchospora alba* were present in most 1 m. quadrats. *Myrica* was confined to the lake flats. *Calluna*, very generally present even in the "average" slopes, was more prominent though still stunted on the steeper slopes. *Narthecium ossifragum*, the bryophytes, and lichens, particularly *Rhacomitrium lanuginosum* and *Cladonia sylvatica* seemed to avoid the lake flats.

The observed pH values were:

	Lacustrine peat	Gentle slopes	Steeper slopes
pH	5·38, 5·34	4·69, 4·63	4·42, 4·40

The high pH of these samples is remarkable in comparison with the figures recorded for *Calluna* and cotton-grass moors.

(3) *Lacustrine bogs*. The bogs developing round small non-calcareous lakes and moorland pools form a fairly definite group of soils with points of resem-

blance to those just considered. The examples described in Table IV are all derived from "reed swamps" of *Carex inflata* often associated with *Equisetum limosum* and *Menyanthes trifoliata* (*Carex lasiocarpa* replaces *C. inflata* in Connemara). The table therefore begins with examples showing the condition of the mud in these reed swamps. Particular attention should be given to the high *p*H values of this peaty mud. In terms of *p*H alone, soils of peaty moorland pools are not necessarily distinguishable from those of *Typha* or *Phragmites* swamps (cf. Misra, 1938), and experience suggests that any submerged soil with a *p*H below 5 is probably a re-submerged acid terrestrial peat.

The peaty soils developed from these reed swamps (Nos. 74–87) are also only slightly acid, the lowest *p*H being 4·28. They are characterized by the presence of *Myrica* and abundant Sphagna, *Molinia*, *Narthecium*, *Erica tetralix* and *Eriophorum angustifolium* are widely distributed though not necessarily always present in a 1 m. quadrat. The soils are always reducing in character, even at 5 cm. below the surface. There is a general resemblance to the upland bogs (Table III, Nos. 51–58), except that in the latter *Molinia* apparently tends to replace *Myrica*, a tendency also shown in the Maam Cross series.

The last samples in Table IV include three (Nos. 88–90) which probably represent a later development from the type of Nos. 84–87 but which may possibly show the effects of artificial drainage improvement. There is a probability of human interference in the area, which is certainly effective in Nos. 91 and 92, both areas traversed by drains. The dominant *Molinia* here is associated with such species as *Scabiosa succisa* and *Potentilla erecta*, and except for a little *Calluna* has none of the species characteristic of the bogs described. The low *p*H and the high oxidation-reduction potential of drained *Molinia* peat is worthy of note. Were these small lacustrine bogs to be left untouched there is considerable probability that they would tend to develop into "raised bogs". Indeed, the Birket Close samples come from an area including a small raised bog, although the succession from the peaty pools to this raised bog is not now clear. The point is mentioned, however, because this series of records runs on without obvious break into the next series which deals with the details of soil conditions on raised bogs.

(4) *Raised bogs.* Raised bogs or lowland moors are formed mainly by the growth of *Sphagnum*, forming peat in great depths, although other species play an important part in this process (see Osvald, 1923). In Table V, therefore, Nos. 93, 101 and 111 deal with the conditions in pure *Sphagnum* peat, where the bog moss has filled up old peat cuttings to a considerable depth, at least 1–2 m., and where the peat is firm enough to support a man with ease. Further, Nos. 94, 102 and 112, represent extensive areas where peat is regenerating rapidly. Nos. 94 and 112 have been in their existing condition for at least 30 years, and there is a possibility that No. 94 represents a transition from willow wood to raised bog. All of these stations represent approximately optimum conditions for *Sphagnum* peat accumulation, on a raised bog at least.

The pH resembles that of the more acid parts of lacustrine bogs (pH 4·2–4·3), the soils are "reducing" though the E_5 is generally, perhaps, rather higher and the vegetation covers the same range of species. For comparison with these figures, it will be found that the central areas of these bogs, with *Eriophorum vaginatum* and *Calluna* usually nearly as abundant as *Sphagnum*, have a much lower pH value (below 4·0) and their E_5 value at 10 cm. tends to approach more nearly the level at which oxidation is detectable (Nos. 95, 103, 108–110, 113–116, 120–122).

Table V. *Raised bogs* (Sphagnum *peat*)

			pH	E_5	Thiocyanate
93	Rusland Moss	Old cutting, *Sphagnum* d, *D*, *O*	4·62	130*t*	0/1
94		Regenerating, *Sphagnum* a, *A*, *M*, *N*, *O*, *T*	4·26	230*t*	1/2
95		Centre, *Sphagnum*, *E*, *C*, *N*, *T*	3·83	270*t*	1/2
96		*Eriophorum vaginatum*, tussock base	3·76	390*t*	2
97		*Calluna* with *Betula* seedlings (drained)	3·65	420*t*	3
98		*Pinus sylvestris*, *Vaccinium Myrtillus*	3·15	460*t*	2
99	Birket Close	Peaty stream, *A*	5·24	230*	1/2
100		*Sphagnum* and *Potamogeton polygonifolius*	5·07	220*	1/2
101		*Sphagnum*, in old cutting	4·25	280*	0/1
102		*Sphagnum*, *A*, *E*, *M*, *N*, *R*, *T*, quaking	4·17	310*	2/3
103		Centre, *Sp* = *E* = *C*, *N*, *T*	3·82	340*	2
104		*Eriophorum vaginatum*, tussock base	3·75	385*	2
105		Bare peat, *Rhynchospora*, *Drosera*	3·42	180*	1/2
106		*Calluna* + 30-year-old birch, drained	3·56	420*	2
107		Bank along drain, *Vaccinium Myrtillus*	3·28	475*	3
108		*Sp* = *C* = *T*, *E*, *N* 5 cm.	3·69	390*	2
109		,, ,, 8 cm.	3·86	270*	1/2
110		,, ,, 14 cm.	3·94	260*	1/2
111	Stribers Moss	*Sphagnum*, in cutting	4·35	190	0/1
112		Regenerating, *Sp*, *A*, *D*, *M*, *N*	4·20	270	1/2
113		Centre, *Sp* = *C* = *E*, *N*, *R*, *T*	3·79	240	1/2
114	Birker Moss	*Sp* = *E* = *T*, *A*, *C*, *N*	3·70	320	2/3
115		*Sp* = *E*, *T*, *A*, *C*, *N*, *R*	3·60	350	2
116	Solway Moss	Centre, *E* = *C*, *Sp*, a	3·47	350	—
117		*Calluna*, d	3·41	435	—
118		*Molinia*, *Calluna*, a	3·46	400	—
119		*Eriophorum vaginatum*, *Sp*, f	3·40	370	—
120	Racks Moss	Centre, *Sp* = *E* = *C*	3·68	230	—
121		Centre (apparently drier)	3·50	370	—
122		Centre, little *Calluna*	3·45	220	—
123		Cut peat with *Molinia*	3·26	415	—
124		*Eriophorum vaginatum*, a; *Sp*	3·41	340	—
125		Birchwood, *Dryopteris-Oxalis*	3·63	450	—

t = samples kept under toluol. * = field measurements.

Symbols used: *A*, *Eriophorum angustifolium*; *E*, *Eriophorum vaginatum*; *C*, *Calluna vulgaris*; *D*, *Drosera* spp.; *M*, *Myrica Gale*; *N*, *Narthecium ossifragum*; *O*, *Oxycoccus quadripetala*; *R*, *Rhynchospora alba*; *Sp*, *Sphagnum* sp.; *T*, *Erica tetralix*.

The series for different raised bogs in Table V illustrate some additional points. In that for Rusland Moss, No. 97 is a drained area with *Calluna* dominant, while No. 98 is an old and extensive sub-spontaneous pine wood also on drained peat. As compared with No. 95, the centre, both show the increase in acidity and rise in E_5 potential which follows drainage. Nos. 96 and 104 show the condition in the peat at the base of *Eriophorum vaginatum* tussocks on different "mosses". Otherwise the results for Birket Close, while

confirming points already mentioned, are mainly of interest because they were done in the field. Nos. 105 and 106 are for a partly retrogressive area and No. 105 refers to one of the areas of bare peat with much *Rhynchospora alba* round a peaty pool. The surface probably dries out at times and is then oxidized and the high acidity pH 3·42 is attributed to this, although at 10 cm. the peat was saturated with water and strongly "reducing" (E_5 180 mV.) at the time of the observations. This is an apparent exception to the general rule that the more acid peats are drier and show higher E_5 potentials.

The four samples recorded from the Solway Moss show little difference in pH value, but illustrate the contrast in E_5 values between the centre and the little altered borders on the west towards the river Sark. *Calluna* is dominant on the naturally drained margin, where the peat has a high E_5 potential, 435 mV., indicating oxidation. The potential is lower where *Molinia* is dominant at a lower level. Certain areas among the *Molinia* show blocking of the drainage from the "moss" and in such places *Eriophorum vaginatum* becomes dominant, with *Sphagnum* also frequent or abundant (No. 119) and a lower soil potential. No. 124 illustrates a similar feature on the Racks Moss, where in one corner a large area was cut to a low level many years ago. *Molinia* covers much of the old "made" peat (No. 123), the lower pH as compared with the bulk of the moss being attributed to oxidation. Where the drains have become blocked, *Eriophorum vaginatum* reappears with much *Sphagnum* and a lower soil potential.

In what is apparently the oldest part of this cut area, the drainage has been maintained and a birch wood with *Dryopteris dilatata*, *Oxalis acetosella* and *Mnium hornum* is established. Here the peat is black, amorphous and well rotted. If this peat has passed through a *Molinia* stage (as one might expect) then it seems probable that long continued oxidation might lead to reduction in acidity or increased pH.

DEVELOPMENT OF ACIDITY

On the whole, however, numerous examples have shown that, in general, oxidation in these damp peaty soils leads to increased acidity. Thus when such soils are drained, both the hydrogen-ion concentration and the oxidation potential increase, presumably as a result of the increased oxidation resulting from replacing water by air. The evidence is clear that the distance of the sample from the soil surface (i.e. the air) partly determines the pH value (cf. also Salisbury, 1922, data for oxidizing woodland soils). Here again the lower pH values near the surface are associated with higher oxidation potentials. This is, in fact, not altogether surprising as the H ion itself can be regarded as an oxidation product (see Part I, p. 182). Moreover, soils which (like lake muds) have always been waterlogged never appear to be very acid even in the most heathy surroundings and are normally above pH 5·3 (cf. Table IV, and Misra, 1938). These muds only develop acidity when their surface is exposed to the

air, a conclusion already drawn in Part II and equally well illustrated by the data in this paper (see Table IV).

These various types of evidence suggest then that we can, under certain conditions at least, use the pH value as a guide to the degree of oxidation a wet soil undergoes. Such a proposition can be examined only in soils with a similar percentage of organic matter. Those mentioned in this paper are (with a few named exceptions) highly organic and probably always contain 90 % of organic matter. Even so, it is possible that another variable may enter into the matter, namely, the composition and hydrogen-ion concentration of the plant residues forming the peat. Thus it is possible that on death *Eriophorum vaginatum* may give more acid material than most species of *Sphagnum*. Finally, it should be recognized that, in drier soils at least, oxidation may finally result in destruction of organic matter and in reduced acidity (see Table V, No. 125 and Olsen, 1923), and for reasons such as this it may be necessary to assume that high acidities indicate either partial or incomplete oxidation or special types of oxidation such as many of those due to moulds. On the whole, however, little exception can be taken to the conclusion that in similar wet soils, a lower pH value is an index of greater oxidation. Further, although there are undoubtedly seasonal drifts in the pH value of a given soil, on the whole this value appears to be less subject to change owing to the conditions prevailing at the time of sampling and during that process. Hence the pH value may often serve (in soils of the highly organic type described) as a better guide to the soil equilibrium than does the E_5 potential which is liable to more rapid change.

The acidity of raised bogs

It will be seen that the consideration of these factors suggested that moorland peats derived from purely aquatic habitats might never become very acid if they remained saturated with water. For this reason, the examination of "mosses" or raised bogs (see p. 299) was attended with particular interest—not only because they represented peats of the required type—but also because in this type of habitat the water in the peat is directly derived from atmospheric precipitation and so is free from bases of telluric origin. If a relatively high pH was found in such a soil it could not, therefore, be attributed to the flushing or neutralizing effects of land drainage, but must rather be ascribed to the failure of acids to develop under waterlogged conditions.

The first examples examined were from the Lake District and they were not very decisive because the "mosses" concerned showed a good deal of marginal cutting and some drainage. Efforts were therefore made to sample other representative and little altered raised bogs, and these include some from Ireland (apparently unnamed) and some from around the Solway Firth. For the purposes of comparison, five (1 sq. m.) quadrats were examined for lists of vegetation, peat samples being taken from three of these, at a depth of 10 cm.

The sampling deals only with the representative central part of the bog. As one could be more certain of finding bogs with marginal cutting in most areas examined, an example of this type was included in each case. Actually, unless there are very definite signs of drainage, there is little (if any) difference between the average pH of such a "moss" or bog and that of an adjacent untouched one. The full vegetation data for the different areas studied are given in the Appendix.

The following table summarizes the pH data and gives also the approximate annual rainfall (in cm.) of the districts concerned:

Bog	pH values	Approximate annual rainfall (cm.)	Remarks
Ireland:			
Galway 1	4·45, 4·37, 4·31	110–120	Quaking—little altered
Galway 2	4·35, 4·32, 4·30		Margins partly cut
South-east of Rochford Bridge	4·10, 4·02, 3 91	85–95	Very extensive—untouched
East of Mullingar	4·08, 3·90, 3·86		Smaller, margins cut
Solway:			
Glasson	3·68, 3·67, 3·57	60–70	Wet, little altered
Racks	3·68, 3·55, 3·49	70–80	Margins cut, extensive
Raeburn	3·47, 3·47, 3·43		Extensive, little altered
Solway	3·50, 3·47, 3·40		Margins much cut

The noticeable feature of these results is the appreciable difference in the pH values for different raised bogs. In some cases there are obvious permanent differences in the water content of the bog. Thus, in the Solway area, Glasson Moss is most obviously wetter than the Solway Moss which is said to have "flowed" in historical time, and which has been much cut up in recent years and so is in a dry condition. Raeburn "Flow" resembles the Solway Moss in type although it does not appear to have been modified by cutting. It may also be a moss which has burst and flowed at some time in the past. Further all the mosses examined in the Solway district are more acid than the Irish ones examined. Hence both the vegetation (see Appendix) and the appearances agree with the idea that the drier "mosses" have a lower pH value.

As raised bogs are dependent upon rainfall for their moisture content, it seems possible that a greater rainfall or a greater atmospheric humidity might tend to prevent the desiccation of the surface and hence to prevent the development of acidity. Thus on the whole the average pH values in Table VI appear to run parallel to the rainfall estimates. The decisive effects would no doubt arise mainly not only from the rainfall but also from the frequency and length of the dry periods, if any, since these must be the main factors in causing desiccation, increased oxidation and lower pH values. No doubt a similar relationship might hold in the case of upland moors. In this case, however, the variability of the slopes in different hill regions is so great as to make comparisons difficult. Generally speaking a greater slope will mean better drainage and hence more oxidation. Thus damp peaty soils of a similar organic content will tend to great acidity on the steeper slopes. This is shown well in the data

for the Connemara blanket bog. An accurate comparison between moorland areas of an upland character can only be made, therefore, by allowing for the slope and drainage factors, a most difficult thing to do. It is, however, suggestive that such moors as the heather or cotton-grass moors of the Pennines should occur under conditions of much lower rainfall than the Connemara blanket bogs, e.g. of the order of 90–120 cm. per annum as compared with 150–175 cm. The relatively high *p*H values of the blanket bog peats appeared in short to be related to their almost permanently saturated condition. The Pennine peats, on the other hand, undoubtedly do undergo considerable drying and superficial surface oxidation in summer, and to this their high acidity may safely be attributed. The suggestion that the degree of acidity of a peat, the *p*H value, indicates the equilibrium reached between the effects of waterlogging (whether climatic or topographic in origin) and of oxidation is thus in harmony with the facts available, though various other and obvious lines of enquiry need to be followed before it can be completely accepted.

General conclusions

The results of this survey may be examined most conveniently in the following tabular summary of the typical conditions recorded for the different major communities.

Table VI

No.	Community	*p*H	E_5	
1	*Calluna* moor	3·4–3·7	450–470	Oxidizing
2	*Vaccinium Myrtillus*	2·8–3·3	410–470	
3	*Carex inflata*	5·3–5·8	100–240	Sub-aqueous
4	*Sphagnum-Myrica* with *Molinia*	4·3–5·6	110–270	Nos. 51, 52, 78–87
5	Blanket bog	4·3–5·4	Probably below 350	—
6	Raised bogs	3·4–4·4	230–350	—
7	*Sphagnum-Calluna* with cotton grass	3·4–4·2	270–390	Nos. 55, 67, 88–90
8	*Eriophorum vaginatum* moor	3·2–3·4	270–390	—

This summary shows that the *Calluna* and *Vaccinium Myrtillus* peats (with or without birch and pine) are characteristic of oxidizing soils which are not (by the tests employed here) distinguishable from those described for woodlands in the second paper of this series. It is assumed, moreover, that no serious oxygen deficiency can be detected in these soils.

The remaining soils described belong to a group which is either reducing (particularly Nos. 3–5 above) or more acid and also slightly oxidizing at times (Nos. 6–8 above). An E_5 of 390 mV. is used in the above summary to indicate that these soils are usually below 400 mV. On the other hand, mainly oxidizing soils seem usually to be above this E_5 level. These figures refer, of course, to a soil depth of approximately 10 cm. and because of the variation of E_5 with depth (and probably with season, see Remesov, 1929, especially) it is necessary to emphasize their approximate nature, in relation to such features as rooting conditions for example. It is assumed, however, that all these soils tend to

suffer from oxygen deficiency below 10 cm. and that oxidation is confined mainly to the superficial layers. Various arguments suggest that increasing acidity and oxidation are connected. Besides the above features, the soils are as a class without nitrate and they usually give feeble thiocyanate reactions, probably because of the scarcity of adsorbed bases in general and of iron in particular. The high organic content (over 85 %) is associated with low drifts in potential when the peats are transported to the laboratory. Both the potential drift and the intensity of the thiocyanate reactions are greater in soils of this type which have been subjected to oxidation in nature and especially in the *Calluna* moor and *Vaccinium* soils.

The vegetation of these "reducing or feebly oxidizing" soils (Nos. 4–7 in Table VI) is remarkable chiefly for its very mixed character. Usually two or three species are abundant, and strictly speaking no easy subdivision of the vegetation types can be made because they tend to grade imperceptibly one into another. Though the Connemara blanket bog and the raised bogs occupy quite definite habitat types, their vegetation merges into a common continuous series. The arbitrary limits which can be assigned to the *p*H ranges of the different species should be used with some caution and the limit between vegetation types at about *p*H 4·3 given in Table VI above is based mainly on the blanket bog and raised bogs and used for convenience in handling the data. Further the 1 sq. m. quadrat may be rather small for some of the mixed upland moors and bogs in the sense that a larger quadrat would include more of the species with a high "constancy" in distribution. Generally speaking, however, *Myrica* and *Molinia* tend to be both more abundant and characteristic of the higher end of the *p*H range, and *Eriophorum vaginatum* (perhaps with *Empetrum nigrum* and *Oxycoccus quadripetala*) more abundant at lower *p*H values. The characteristic species of these communities are, however, probably the Sphagna, and such species as *Eriophorum angustifolium*, *Narthecium ossifragum*, *Erica tetralix* and perhaps *Scirpus caespitosus* which have at best a lower frequency but a higher "constancy" than the species already mentioned. The position of *Molinia coerulea* in this series is particularly interesting. It may apparently occur as a prominent member of a plant community either on reducing soils above *p*H 4·4 (approx.) or on oxidizing soils below *p*H 3·9. Its associates in the former case have been indicated above. It is, of course, possible that the common feature of habitats so different is some factor such as the normal scarcity of nitrates or available nitrogen. More generally, however, it is quite possible that the absence of oxygen above *p*H 4·4 may be, in some respect, equivalent to the effects of higher acidity. Putting it in another way, high acidity may be supportable only when oxygen is present. There are indications that other species may show similar relations to *Molinia* in these respects.

Summary

On the basis of the pH and values obtained from electrical potentials and thiocyanate tests at 10 cm. depth, a distinction is made between four main types of moorland and bog soils, namely:

(1) Oxidizing soils below pH 3·8 with *Calluna vulgaris*, *Vaccinium Myrtillus* or *Molinia coerulea* dominant.

(2) Reducing soils between pH 5·5 and 4·4 (approximate)—mixed vegetation of blanket bog or lacustrine bog type.

(3) Soils, feebly oxidizing at times, between pH 4·4 and 3·4 (approx.)—vegetation of mixed types of upland moor or raised bog.

(4) Soils feebly oxidizing at times—below pH 3·4—vegetation of cotton-grass moor.

The development of soil acidity in these highly organic soils is associated with oxidation.

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APPENDIX

Data giving species representative of typical areas in raised or blanket bogs

	Blanket bog			Raised bog							
	Lacustrine	Average	Steep slope	Galway 1	Galway 2	Rochford Bridge	Mullingar	Glasson	Rachs	Raeburn	Solway
Sphagnum spp.	5	5	5	5	5	5	5	5	5	5	5
Calluna vulgaris	.	4	5	4	4	5	5	5	4	5	5
Erica tetralix	4	5	5	5	5	5	5	5	5	3	5
Empetrum nigrum	.	.	.	.	+	.	.	.	.	3	1
Andromeda polifolia	.	.	.	5	5	4	2	5	4	3	5
Oxycoccus quadripetala	.	.	.	3	3	2	4	2	1	5	5
Eriophorum angustifolium	4	2	2	5	5	5	4	5	4	3	4
E. vaginatum	.	+	1	.	1	+	2	5	5	5	5
Scirpus caespitosus	2	.	1	2	2	3	3	1	3	1	1
Narthecium ossifragum	.	3	5	5	5	5	5	3	4	1	1
Rhynchospora alba	3	5	3	5	5	3	1	5	2	.	.
Drosera spp.	.	3	2	3	2	3	2	2	1	.	1
Carex panicea	2	.	.	1	1	1	.	1	.	.	.
Hypnum cupressiforme	.	.	.	3	2	1	2	.	1	2	2
H. Schreberi	.	.	.	.	.	.	1	1	.	2	.
Rhacomitrium lanuginosum	.	4	5	.	1	.	1	.	.	1	1
Dicranum scoparium	.	1	.	.	1	.	.	.	1	1	.
Leucobryum glaucum	.	1	2	1	.	.	.	1	.	1	.
Pleurozia purpurea	.	2	3	2	1	.	.	.	.	.	.
Cladonia sylvatica	.	5	5	4	4	4	2	2	2	5	5
C. uncialis	.	2	.	3	3	1	.	1	2	1	1
C. coccifera	.	.	.	1	.	.	2	.	.	2	2
Schoenus nigricans	4	5	4	.	.	.	.	.	.	.	.
Molinia coerulea	5	5	5	.	.	.	.	.	.	.	.
Myrica Gale	5	.	.	.	.	.	.	.	.	.	.
Campylopus atrovirens	.	3	2	.	.	.	.	.	.	.	.
Polygala serpyllacea	.	.	3	.	.	.	.	.	.	.	.
Utricularia minor	.	.	.	1	.	.	.	.	.	.	.
Menyanthes trifoliata	1	.	.	1	.	.	.	.	.	.	.
Batrachospermum sp.	.	.	.	+	.	.	.	.	.	.	.
Lycopodium Selago	.	.	.	.	.	.	1	.	.	.	.
Aulacomium palustre	.	.	.	.	.	.	1	.	1	1	.
Webera nutans	.	.	.	.	.	.	.	.	1	1	.
Polytrichum commune	.	.	.	.	.	.	.	.	.	1	.

Five quadrats taken for each locality, the numbers refer to the number of quadrats in which the given species was found, the plus sign signifies presence near the quadrats.

OBSERVATIONS ON *FUCUS SERRATUS* L. KEPT UNDER LABORATORY CONDITIONS

By M. B. HYDE

(*With three Figures in the Text*)

Introduction

Almost all those who have investigated the metabolism of marine algae have used freshly obtained material, frequently renewed, in order to avoid the possible adverse effects of laboratory conditions. Ehrke (1931) working with *Fucus serratus* used fresh material daily in summer, but in winter the same plant in a series of experiments lasted 8–10 days. Kniep (1915), however, stated that he kept *F. serratus* successfully for 5 months (March to August), in darkness, changing the sea water "frequently", and that the plants remained completely fresh ("völlig frisch") throughout.

More recently Lampe (1935) has done experiments on the rate of assimilation of *F. serratus*, keeping plants at a constant temperature for as long as 7 weeks, and he has recorded no change in the assimilation rate under certain conditions of light and temperature (using artificial light when measuring the assimilation).

In connexion with experiments on the effect of light and temperature on the rate of apparent assimilation of *F. serratus* (see Hyde, 1938), consecutive observations have been made of material kept in the Botanical Laboratory at Westfield College for nearly twelve months, from July 1935 to the end of June 1936. The interest of these observations lies:

(1) in connexion with the changes in the thallus itself;

(2) in the relatively steady rate of carbon assimilation when determined under comparable conditions.

The *F. serratus* was obtained from the shore at Bexhill from the middle of the *F. serratus* zone. Several small pieces (see Fig. 1), each with two dichotomies, were cut from a young, non-fertile plant and kept in two glass vessels of sea water, holding about a litre, partially covered to reduce evaporation yet allow for ventilation. Four of these fronds, B, B_1, C and D were kept under observation for some time. In July 1935 the dish containing fronds B and B_1 was placed on a north-facing balcony which received no direct sunlight, and the other dish, with frond C, underneath the bench of an adjoining room with north windows. Temperatures were recorded daily, and in the hot weather

(8 July to 23 August 1935), the bowls were surrounded each morning by a mixture of ice and water. The temperature of the water in the bowls thus varied from 8–10° C. by day to 15–17° C. at night, frequently reaching 20–21° C. at the week-ends during the hot weather, ice not having been provided on Sundays. It was found that inside the building in July, between noon and 3 p.m., with a light intensity of about 0·1 % total daylight (see p. 318), and at the

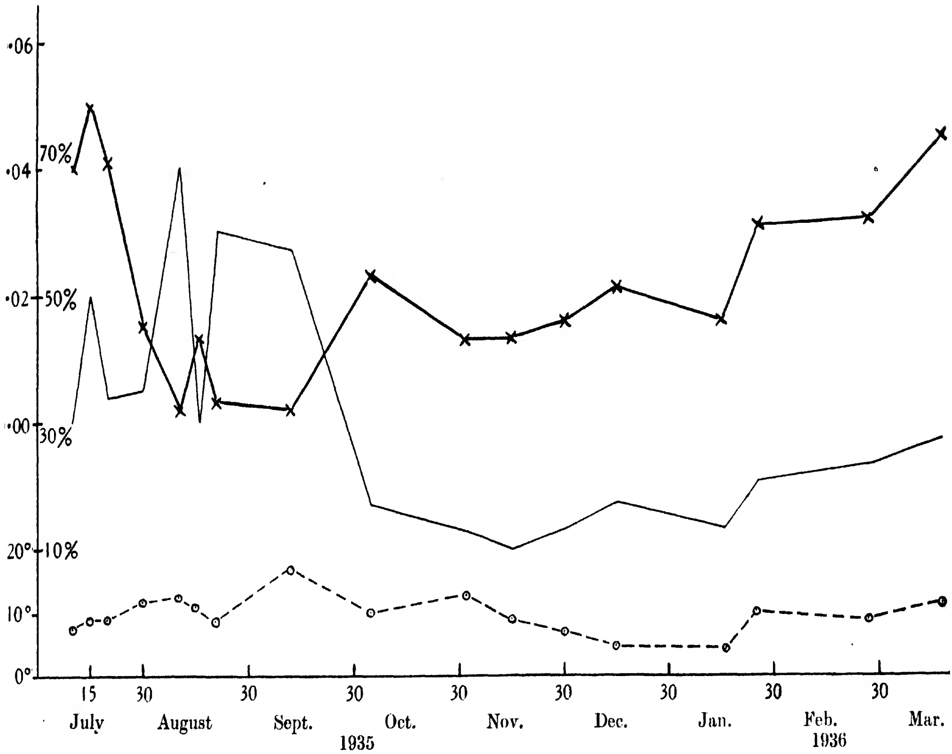

Fig. 1. Rate of apparent assimilation of *Fucus serratus* compared with relative light intensity and temperature.

Apparent assimilation, × — × — × ; light intensity (%), ——— ; temperature, ⊙—⊙—⊙.

particular experimental temperature used (8–10°), there was in frond C little or no excess assimilation over respiration, while outside with frond B, where the light intensity varied from day to day according to the weather, the rate of apparent assimilation varied with the amount of light available, it being more rapid on sunny days than on days with overcast skies. (See Fig. 1, July 1935, and Table II.)

The lengths of time for which the various fronds remained alive are shown in Table I.

Table I. *Length of time for which the different fronds of* Fucus serratus *remained alive*

Frond	When collected	Conditions*	Length of time in laboratory
B	July 1935	Outside, north light	1 year†
B_1	July 1935	Outside, north light	4 months
C	July 1935	Inside (0·1% total daylight)	1 month
D	Oct. 1935	Outside, north light	9 months†

* During the cold weather of winter, i.e. from the end of December 1935 onwards, the fronds *B* and *D*, which had been kept outside until then, were brought indoors and kept near a north-facing window in an unheated north room. They remained inside throughout the spring. (The actual assimilation experiments were always done on the balcony, throughout the winter.)

† These fronds were still alive at the end of June 1936, when observations ceased.

Course of carbon assimilation

(*a*) *Method*

The measurement of the assimilation rate was carried out every day at first, between 12 noon and 3 p.m. (summer time), under natural conditions of illumination in the two places (i.e. on the balcony and inside). The relative light intensity (measured by means of a Wynne "Infallible" Exposuremeter placed horizontally at level of thallus) was expressed as a percentage of total daylight, the light intensity at noon (i.e. 1 p.m. summer time) on a bright sunny day in July being taken as 100%, when 5 sec. was the time required for the sensitive paper held horizontally to reach the darker standard tint.

The temperature during the experiments was 8–10° C. during the winter and summer, and 10–14° C. in spring.

The amount of apparent assimilation was measured by determining the amount of oxygen given out in a known time, using Winkler's method (see Harvey, 1928). Each assimilation chamber consisted of a flat-sided glass bottle, holding about 150 c.c., with a close-fitting stopper, and whose capacity had been accurately determined. Two experimental bottles, *B* and *C*, each containing a piece of *Fucus* frond of known area, and a third bottle, *A* (containing no *Fucus*), were filled from a large bottle with sea water which had been deoxygenated by allowing some other *Fucus* to respire in it overnight, so that on assimilation there should not be an excess of O_2, causing the formation of bubbles. (Blank experiments had previously shown this method of removing oxygen to be satisfactory, while at the same time the *p*H was not too much reduced by the CO_2 of respiration.) By gently agitating the water in the large bottle before use it was assured that all three experimental bottles received sea water of the same composition.

The two flat-sided bottles *B* and *C* were placed horizontally in the glass bowls containing the *Fucus*, one on the balcony and the other under the bench of an adjoining room, so that they were just submerged. Bottle *A* was placed in the dark. The temperature and light intensity were observed at intervals

during the three hours that each experiment lasted. The bottles *B* and *C* were then brought inside, the fronds of *Fucus* removed, and the titration carried out, a constant procedure being employed to standardize gains or losses of oxygen during the operation. The difference of the oxygen content of the water in bottles *B* and *C* and that in *A* gave the amount of apparent assimilation that had taken place. It was calculated as grams of oxygen liberated per litre per 100 sq. cm. of frond *in three hours.*

Table II

Date	Temp. (° C.)	Relative light intensity	Apparent assimilation (as O_2 g./l./100 sq.cm./3 hr.) Frond *B*	Frond *D*
Period 1:				
10. vii. 35	7·5	30·0	0·0405	—
11. vii. 35	9·0	30·0	0·0434	—
12. vii. 35	8·0	40·0	0·0505	—
13. vii. 35	9·0	50·0	0·0623	—
14. vii. 35	8·5	44·0	0·0412	—
15. vii. 35	9·0	50·0	0·0497	—
16. vii. 35	8·0	24·0	0·0317	—
17. vii. 35	9·0	40·0	0·0346	—
18. vii. 35	9·0	34·0	0·0448	—
19. vii. 35	9·0	34·0	0·0413	—
Period 2:				
31. vii. 35	12·0	35·0	0·0417	—
2. viii. 35	7·5	40·0	0·0059	—
7. viii. 35	17·0	50·0	0·0058	—
12. viii. 35	12·0	70·0	0·0016	—
16. viii. 35	11·5	30·0	0·0137	—
21. viii. 35	9·0	60·0	0·0035	—
12. ix. 35	17·0	57·0	0·0026	—
Period 3:				
8. x. 35	10·0	17·0	0·0227	0·0328
9. x. 35	10·0	25·0	0·0211	0·0347
10. x. 35	10·0	35·0	0·0301	0·0392
11. x. 35	11·0	36·0	0·0276	0·0378
14. x. 35	14·0	30·0	0·0274	0·0338
16. x. 35	14·0	15·0	0·0224	0·0350
21. x. 35	5·0	20·0	0·0172	0·0321
23. x. 35	7·5	19·0	0·0162	0·0313
2. xi. 35	13·0	12·5	0·0116	0·0287
5. xi. 35	9·0	18·0	0·0217	0·0317
16. xi. 35	8·5	10·0	0·0115	0·0197
21. xi. 35	8·5	12·0	0·0184	0·0219
29. xi. 35	7·5	12·5	0·0179	0·0254
5. xii. 35	3·0	12·5	0·0154	0·0224
16. xii. 35	4·5	17·0	0·0207	0·0233
Period 4:				
16. i. 36	4·0	12·5	0·0177	0·0265
22. i. 36	7·0	15·0	0·0314	0·0336
28. i. 36	10·0	20·0	0·0305	0·0378
8. ii. 36	4·0	16·0	0·0260	0·0392
20. ii. 36	10·0	20·0	0·0311	0·0414
27. ii. 36	9·0	22·5	0·0319	0·0400
7. iii. 36	10·0	20·0	0·0329	0·0448
19. iii. 36	11·0	26·5	0·0446	0·0586
Period 5:				
25. iv. 36	15·0	30·0	0·0576	0·0493
4. v. 36	15·0	50·0	0·0552	0·0615
19. v. 36	10·0	33·0	0·0379	0·0550
20. vi. 36	25·0	50·0	0·0401	0·0320

After the experiment the fronds *B* and *C* were returned to their respective glass vessels until the next day.

The experiments were carried out daily for ten days (10 to 19 July), at the end of which time there was no apparent falling off in the assimilation rate. Through the co-operation of Dr E. M. Delf, and Miss M. T. Martin, the rate of assimilation was measured at intervals throughout the summer vacation. In July and August the sea water needed frequent renewal. In spite of the use of ice, a bacterial film formed on the surface in one to three days, and signs of decomposition appeared at the edges of the *Fucus* fronds, the water taking on a brownish tint. On such occasions, the thallus was removed, washed in sea water, and given fresh cooled sea water in a clean dish. Owing to shortage, the same sea water was used more than once, but was first well boiled, filtered, cooled and lightly charged with carbon dioxide by the addition of 3–5 c.c. of soda water per litre.

From October 1935 onwards, the frond *B*, and another frond *D* (brought from Bexhill on 6 October) were subjected to more or less continuous observation, and the rate of assimilation was measured at intervals of 7–10 days.

(*b*) *Results*

The results shown in Table II are depicted graphically on p. 317.

It is seen from Table II and from Fig. 1 that the rate of apparent assimilation *per* 100 *sq. cm.*, which had fallen during the summer months from about 0·04 g. O_2/l. to about 0·01 g./l., rose in October more nearly to its original value (to 0·025 g./l.), and there appeared to be a linear relation between the light (which was not very bright) and the assimilation rate, the temperature of the experiments in each case being about 10° C. This relation between assimilation and light intensity can be seen more clearly in Table III, which gives the values for frond *B* only (compare also Fig. 1, July).

Table III. *Relative assimilation and light intensity in July and October* 1935. (*Experiments with frond B*)

	10–19 July	8–16 October	Ratio July/October
Relative light (% daylight)	c. 40	c. 25	1·6 : 1
Apparent assimilation	c. 0·04	c. 0·025	1·6 : 1

During August, however, it was noticed that on very sunny days (see 12 and 21 August on the graph, when the light intensity was 70 % and 60 % respectively), the rate of assimilation was much less than on less bright days (0·0016 g./l. on 12 August (light 70 %, temperature 12·5° C.), as compared with 0·0137 g./l. on 16 August (light 30 %, temperature 11·5° C.)). It therefore seems that not only is the plant incapable of using all the light available at high light intensities, but that strong light reduces the rate of assimilation as performed at these intensities.

When the weather was very cold, as on 5 December, the rate of assimilation was 14 % less than at the same light intensity a few days earlier (29 November), probably owing to the lower temperature (3° instead of 7·5° C.) having a retarding effect (see period 3 of Table II and graph).

In the spring of 1936 (January to May) as the days became more sunny, the rate of apparent assimilation *per square cm.* rose in both fronds *B* and *D* (see period 4 on Table II and graph), corresponding to an increase in the light intensity, while the air temperature remained comparatively low. During February, although frond *B* had decreased further in area, suffering more loss from slow decay than could be replaced by growth in length, its rate of apparent assimilation per 100 sq. cm. reached the same value as in October 1935, while that of frond *D* sometimes exceeded the October value.

Towards the end of March, during a spell of very sunny weather, and again in May 1936, the rate of assimilation (see, for example, the experiment on 19 March, light intensity 26·5 %) in both fronds *B* and *D* greatly exceeded the rate at the same light in October, and in the case of *B* was as great as with a light intensity of 35 % in July (see Table II), suggesting that the brighter days of late March 1936 were having an accelerating effect on the assimilation rate which was more marked after the dull days of winter than in July and October, when the plants had just been brought from bright light on the shore.

It is to be expected that the conditions of light, etc., under which the plant has been living will affect its subsequent assimilatory reaction. The position of *F. serratus* as a "sun plant" has already been discussed (Hyde, 1938), and it need only be pointed out here that after a period of relatively dull light a typical sun plant responds to an increase in light intensity with an increase in the assimilation rate. *F. serratus*, however, cannot give this response in light intensities above two-thirds of total daylight (Hyde, 1938), and the experiments of August 1935 now described indicate that here the daylight also was too bright to allow the maximum assimilation to take place.

This maintenance of the original rate of assimilation of *F. serratus* over a considerable period of time is interesting because, although growth in length took place, in this case the hot weather had caused a considerable proportion of the lamina of frond *B* (46 % of the total surface area) to decay away (see Fig. 2), and it is in this region that the largest proportion of assimilating cells is to be found, the midrib region—except for the superficial layers—being concerned in other functions.

BIOLOGICAL CHANGES

In spite of the precautions taken during the hot weather (July and August), decay set in and gradually extended towards the midrib, beginning in superficial cells at or near the margin. The material was collected on the shore at Bexhill late on 7 July, received by post and placed under observation on the morning of 8 July, being kept submerged all the time. By 2 August the frond *B*,

on the balcony, had become brittle rather than absolutely flexible. Frond C, which had been kept indoors in dim light, had soft gelatinous decomposing regions, and so was thrown away. Whilst remaining healthy in appearance, frond B showed one or two lighter patches on 12 August; these had extended towards the midrib by 24 August. The edges appeared ragged and colourless on 12 September. By 8 October a considerable proportion (16 %) of the lamina had decayed away, but the midrib was firm and brown and towards the base was covered with green epiphytes. These were scraped off and the whole surface gently scraped before the assimilation rate was again measured.

From 6 October onwards the frond was subjected to more or less continuous observation. The weather was colder and there was no need for ice to keep the

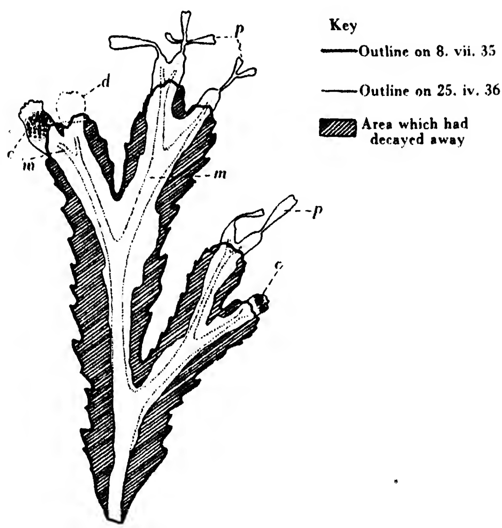

FIG. 2. Changes which occurred in frond B during $10\frac{1}{2}$ months. p, proliferations; c, conceptacles; m, outline of midrib; d, tip detached 16. i. 36.

temperature of the sea water at 10° C. The sea water in the glass vessel was changed once a week, fresh supplies of sea water being obtained regularly from Plymouth. The rate of apparent assimilation was measured at similar intervals, and compared with that of a similar piece of *Fucus* (frond D), part of a similar plant brought from Bexhill on 6 October. Both fronds B and D were carefully watched and gently scraped at intervals to remove any film of epiphytes or bacteria there might be. A greenish tinge in reflected light, at one point thought to be due to green epiphytes, was shown to be present also in new fronds, just received from the shore, and appears to be due to a kind of fluorescent reflection from the surface cells. Sections cut in October of a frond B_1, twin to B, which had been kept under the same conditions, showed that in B_1 the assimilating zone was still as compact as in a fresh frond, and that there were no epiphytes nor endophytes present inside the thallus.

By 20 October conceptacles had begun to develop on two of the tips of the old frond *B* and signs of more developing were seen on 21 November, when three of the tips had begun to proliferate (see Fig. 2). The conceptacles increased in size and number throughout the term, and by 20 December they were raised from the surface as small, conical lumps. The frond still remained brittle, and on 16 January 1936, one of the fertile tips was accidentally broken off. Sections cut of this tip showed that the conceptacles were female, containing oogonia in various stages of development, in some the contents having divided to form eight eggs.

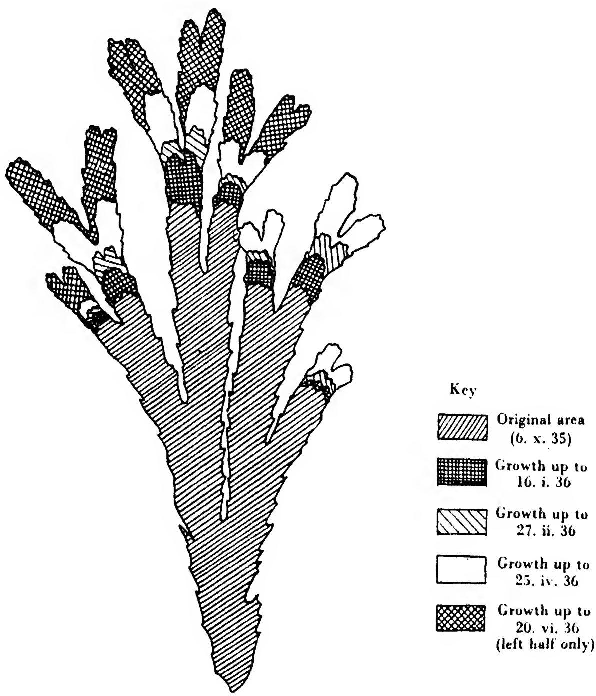

Fig. 3. Increase in area of frond *D* due to growth in length.

Some slight decomposition of this frond *B* was still taking place peripherally, probably due to its being thoroughly infected with bacteria during the hot weather, but the main part of the frond that was left remained firm and healthy.

As time passed, however, frond *B* began to look less healthy. The continued scraping necessary to remove bacterial films etc. roughened considerably the surface of the frond, and during February 1936 a reddish brown colour developed in the peripheral regions. Kniep (1915) observed a similar reddish coloration, which he attributed to age and decomposition, and it seemed probable that frond *B*, although fertile, was near the end of its life.

It is of interest to note here that twenty plants on the shore at Bexhill which were marked *in situ* by means of chicken rings as being mature[1] (i.e. having fertile and discharging conceptacles), in September 1935, had completely died away, except for haptera and stipes, by December 1935. Therefore if frond *B* (taken from the shore in July 1935 from a plant which was not then fertile) had been allowed to remain on the shore, it would probably have died and decayed away completely by December 1935, while in the laboratory it remained alive for more than five months longer.

During the months of January to March 1936 the conceptacles on frond *B* increased considerably in size. On 6 February, when the frond was lifted from the water, a stream of colourless mucilage hung from the fertile tips, but by 20 March no oogonial extrusion had been seen. The oospheres were liberated, however, during the Easter vacation, the first discharge taking place between 1 and 23 April, being first seen on the bottom of the dish when the frond was examined on 23 April, after an interval of 3 weeks. Eggs continued to be shed, apparently a few daily, until 12 May, and then more sparingly at intervals of a few days until 22 May, when liberation ceased. It was thus five months after their initiation (as seen with the naked eye) that the conceptacles on frond *B* became mature, and another month before they had discharged all their contents. This may or may not be a slower rate of development than occurs on the shore, where it was noted at Bexhill that plants marked in early December 1935 as having rudiments of conceptacles just visible to the naked eye showed little change in their condition when examined over a month later, indicating that in nature the development of the conceptacles to maturity is a slow process extending over several months; the rate of development may be dependent on the temperature. Observations at Bexhill show that the sporelings of one winter (December–January) have developed mature conceptacles by the late spring or early summer, shedding their contents between April and October, each individual plant having probably only a short fertile period. Afterwards the plants die away, so that only haptera and stipes are left by the next December. On this shore the plants of *Fucus serratus* appear to be definitely annual. A few plants, however, such as the one from which frond *D* was taken, were not fertile in October, presumably having developed later than the majority of sporelings. These plants are probably the ones which become fertile earliest in the next year (i.e. in April).

The frond *D*, which had been brought from the shore on 6 October, was never at a temperature above 15° C. (generally it was at about 10°, or less during the winter months), and it showed no signs of degeneration or decay of any sort after being kept for over nine months in the laboratory. This shoot, as well as frond *B*, had increased considerably in length (see Fig. 3), its surface

[1] These twenty plants were typical. All the surrounding plants, which were fertile during the summer, appeared to have disintegrated also by December. (It was only possible to examine the plants personally during the vacations.)

area in May 1936 being 30 % more than in October 1935, while by the end of June it was exactly double the size it was in October—see Table IV. Growth was more rapid from February to June than from October 1935 to February 1936. The newly formed tips of the frond *D* were rather paler in colour than the rest of the frond, which, after seven months under laboratory conditions, was barely distinguishable in appearance from a plant growing on the shore. There is a short pale region at the ends of the young tips of *F. serratus* plants when growing *in situ*, so that the pale region at the ends of the frond *D* was a natural appearance, although it extended for rather more than the usual distance down the frond.

The growth in length of the *detached* tips *B* and *D* of *F. serratus* shoots is remarkable, considering that the only nutritive salts are those present in the small volume of sea water, which was renewed weekly.

In frond *D*, in contrast to frond *B*, there were no proliferations from the young ends. These were developed in frond *B* after decay had begun, and may have been regeneration resulting from some change in the physiological nature of the cell contents.

Signs of conceptacles were visible on four of the tips of frond *D* on 19 May 1936, after this frond had been 8½ months under laboratory conditions, and these increased considerably in size and number during the next month. Conceptacles were first seen in frond *B* after three months in the laboratory. Their later development in frond *D* may have been because the plants were not of the same age when brought from the shore, but it is more probable that the development of conceptacles in frond *D* was delayed because all the available nutrient material was being used up in the formation of the new tissue which accompanied the growth in length, this process generally occurring in the life cycle *before* reproduction sets in.

The changes which took place in the various fronds are summarized in the following table (Table IV) and the actual areas given in Table V (p. 326).

Table IV. *Changes in* Fucus serratus *obtained from Bexhill and kept on a balcony from* 8 *July* 1935 *to June* 1936

Date	Frond *B*	Frond *D*
8 July	Placed in position	—
12 Aug.	Paler patches becoming evident	—
12 Sept.	Edges ragged and colourless	—
6 Oct.	16 % lamina decayed away	Obtained and placed in position
20 Oct.	Signs of conceptacles	No change
21 Nov.	Small proliferations at tips	,,
20 Dec.	Conceptacles as raised protuberances	,,
16 Jan.	29 % lamina decayed away. Oogonia segmented	Tips paler. Growth in length
27 Feb.	Mucilage streaming from conceptacles	—
1–23 Apr.	First oospheres shed	Further growth in length
11 May	A few oospheres still shed daily	—
13 May	Oospheres shed less frequently	Signs of developing conceptacles
22 May	No more oospheres shed	—
20 June	No change	Conceptacles larger. Considerable growth

Table V. *Changes in area of fronds* B *and* D

Frond	Date	Area (sq. cm.)	Percentage change
B	9. vii. 35	32·50	—
	8. x. 35	24·00	−16·0
	2. xi. 35	23·20	−18·5
	21. xi. 35	20·88	−25·8
	16. i. 36	19·81	−29·0
	25. iv. 36	17·37	−46·6
	20. vi. 36	17·06	−47·5
D	8. x. 35	34·12	—
	16. i. 36	37·45	+ 9·7
	27. ii. 36	38·32	+12·3
	25. iv. 36	44·80	+31·3
	4. v. 36*	26·55	+31·3
	20. vi. 36*	40·44	+100

* One-half only of frond *D* was measured.

It must be remembered that the conditions under which the *Fucus* had been kept were very different from natural ones, the most important differences which might have an adverse effect being:

(*a*) These shoots depend entirely on the mineral salts present in the small volume of sea water. It is possible that in a Schreiber or other nutritive solution, if successfully applied, degeneration in frond *B* might have been avoided and growth might have taken place more rapidly.

(*b*) The fronds, being under natural conditions of *land* illumination, were in daylight from 5 a.m. to 10 p.m. in the summer, and always during the daylight period there were no intervals of dimmer light of altered composition such as they would experience during submergence on the shore.

According to Poole & Atkins (1926) (i) up to 75 % of the light which has entered the surface is absorbed in the first 5 min.; (ii) all the red rays are cut off in the first 5 min. The above values relate to the water off Plymouth, and are therefore fairly comparable with those for Bexhill.

(*c*) The fronds were kept *permanently* submerged, there being no alternation of submergence and exposure, such as prevails on the shore in the *F. serratus* zone.

In spite of these and other differences from the normal conditions, the rate of apparent assimilation *per unit area* of the frond remained approximately constant over a considerable period, under comparable conditions of temperature and light, and dependent on the light intensity. It seems quite possible, if care were taken during hot weather to prevent decay from setting in —by using sterile sea water, etc.—to supply mineral salts, to keep the fronds under more natural conditions of light and exposure, and to maintain fairly low temperatures (e.g. about 10° C.), that the period of time during which *F. serratus* and other marine algae could be kept healthy under artificial conditions might be considerably prolonged. The moderately low temperature suggested would help to prevent bacterial attack, as well as being more suitable for the physiological processes of the plant at low light intensity.

SUMMARY

1. One frond of *Fucus serratus* has been kept under observation for nearly twelve months.

2. This frond (*B*) decayed away at the edges, reducing the area by 47 %, but the assimilation capacity and the value of assimilation per unit area remained unimpaired, when measured under comparable conditions, from July to January 1936. Later in the spring of 1936 (from March onwards) the assimilation capacity increased, the assimilation rate per 100 sq. cm. being as great as with a much brighter light in the previous July.

In another frond (*D*), which was never at a temperature above 15° C., an increase of 100 % in area was brought about by the growth, the plant exactly doubling its size in nine months, and there was no sign of any kind of decay after over eight months in the laboratory.

3. Regeneration of new vegetative tips occurred from the young ends of the frond *B*.

4. Development of female conceptacles with oogonia took place, the oospheres being liberated about five months after signs of conceptacles were first observed.

5. A great power of tenacity of life was seen.

6. Temperature seems to be an important factor in keeping *Fucus serratus* in the diffuse light of the laboratory conditions.

These experiments arose out of an investigation forming part of a thesis for the degree of M.Sc. in the University of London. The writer wishes to express her gratitude to Dr E. M. Delf, F.L.S., of Westfield College, for the helpful criticism and encouragement she has given throughout the course of this work.

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INFRA-RED PHOTOGRAPH OF ARCTIC BIRCH FOREST AND FELLS

By H. N. SOUTHERN and W. A. S. LEWIS

(*With Plate IV*)

THIS photograph shows the use that can be made of infra-red sensitive plates and films in showing the topography of a wide area of country and the differentiation of the various vegetational areas. This is facilitated by the fact that there is very little reflexion of visual rays from a green surface, whereas the infra-red rays are not only reflected amply but with sufficient differentiation to give a tone contrast between types of vegetation.

The area shown is that south of Abisko and Lake Torne Träsk, Swedish Lappland (lat. 68° 12′ N., long. 18° 20′ E.). The lake itself, which is just to the left of the area shown in the photograph, lies east and west so that the mountain ranges to the south all drain into a series of basins lying roughly north and south. The lake lies at an altitude of 1000 ft. and the surrounding mountains vary between 4000 and 5000 ft., while the photograph was taken at about 3500 ft. The railway, which has been carried through this region over the pass and down to the Norwegian port of Narvik, follows the line of the south shore, and crosses the Abiskojokk river which can be seen in the left foreground.

The main part of the photograph shows the terminal portion of the basin drained by the Abiskojokk, which is fed during the snow melt from the surrounding mountains. One of the tributaries is seen running down towards the main river just under the heavy cap of cumulus at the right-hand end of the picture.

The distance from the camera to the U-shaped glacial valley in the central distance is roughly 15 miles, and the viewpoint is looking directly eastwards parallel with the lake, so that the Abiskojokk river runs straight across the picture, though only a tiny portion of it can be seen on the left emerging from behind the hillside in the foreground.

The area extending from the east bank of the river to the foot of the mountains, which it is the main point of this photograph to illustrate, is a slope rising fairly gently from 1000 to just over 3000 ft., the tree line occurring about the 2000 ft. contour. The nearer portion of this area consists of closed forest with dominant silver birch (*Betula alba* and many subspecies). In general these trees grow to a height of 20 or 30 ft., and their density is somewhat variable: some areas, where numbers of them are dying off, might almost be classed as open associations. The secondary growth of this whole area is characterized

by such woody plants as *Empetrum nigrum*, *Vaccinium vitis-idaea*, *Juniperus sibirica*, *Phyllodoce coerulea*, *Cassiope tetragona*, and *Cornus suecica*.

In the middle of this main area of birch forest can be distinguished the two other main habitats of the lower ground in these regions, which are to some extent phases of the same seasonal succession. The areas that appear the lightest are swamps which have dried to a considerable extent, while the slightly darker areas, which are not quite so sharply differentiated from the surrounding birch, are swamps which still retain a good deal of moisture.

Naturally during the weeks immediately following the snow melt, all these swamp areas are equally wet, but the water drains from some of them more quickly than from others, and there is a corresponding difference in the vegetation at any one time. The damper parts are characterized by a great number of Salices, and by an abundance of showy plants such as *Trollius europaeus*, *Viola biflora*, *Pinguicula vulgaris* and *P. alpina* together with a great number of sedges and grasses.

In the drier swamp areas Salices are again abundant, while *Betula nana* forms great bushes and spreads in from the edges. Woody plants are prevalent, such as *Empetrum*, *Phyllodoce* and *Andromeda polifolia*, while in drier parts such plants as *Rubus chamaemorus*, *Dryas octopetala* and *Astragalus alpinus* appear.

The small lakes, which show up prominently in the photograph owing to the lack of infra-red ray reflexion from blue surfaces, are usually associated with a swamp area and are more or less transient. The larger one, however, in the middle of the picture, which was about a mile in circumference, was permanent with steep banks all around it.

The tree line on such gently sloping ground as this is an irregular affair, characterized by the increasing prevalence of dry swamp areas, and is indicated in the photograph by the rather blotchy area midway between the lake and the mountains beyond. At the foot of the mountains the regular fells are distinct, since the increasing outcrops of rock are shown by dark streaks penetrating into the lighter vegetation. Here there is still a certain amount of sallow, while saxifrages become increasingly common, and such typical plants as *Rubus arcticus* appear.

Finally, in the mountain areas the petering out of the vegetation is visibly demonstrated by the gradual fading away of the light areas, finally giving way completely to the black metamorphic rock. To the left of the glacial valley the lower mountains may be seen with vegetation right up to their summits, except for a certain amount of outcrop, this constituting the typical fell country of the Arctic. Furthermore, on the crag to the right of the same valley it can be seen how the vegetation creeps farther up its side on the sheltered south-western aspect, while on the northward face there is practically none even at the base. This marked distinction between the reflecting power of vegetation and of rock is also shown very clearly in the foreground only some

hundred yards away from the camera, though the heavy cloud shadow closest of all should not be mistaken for rock.

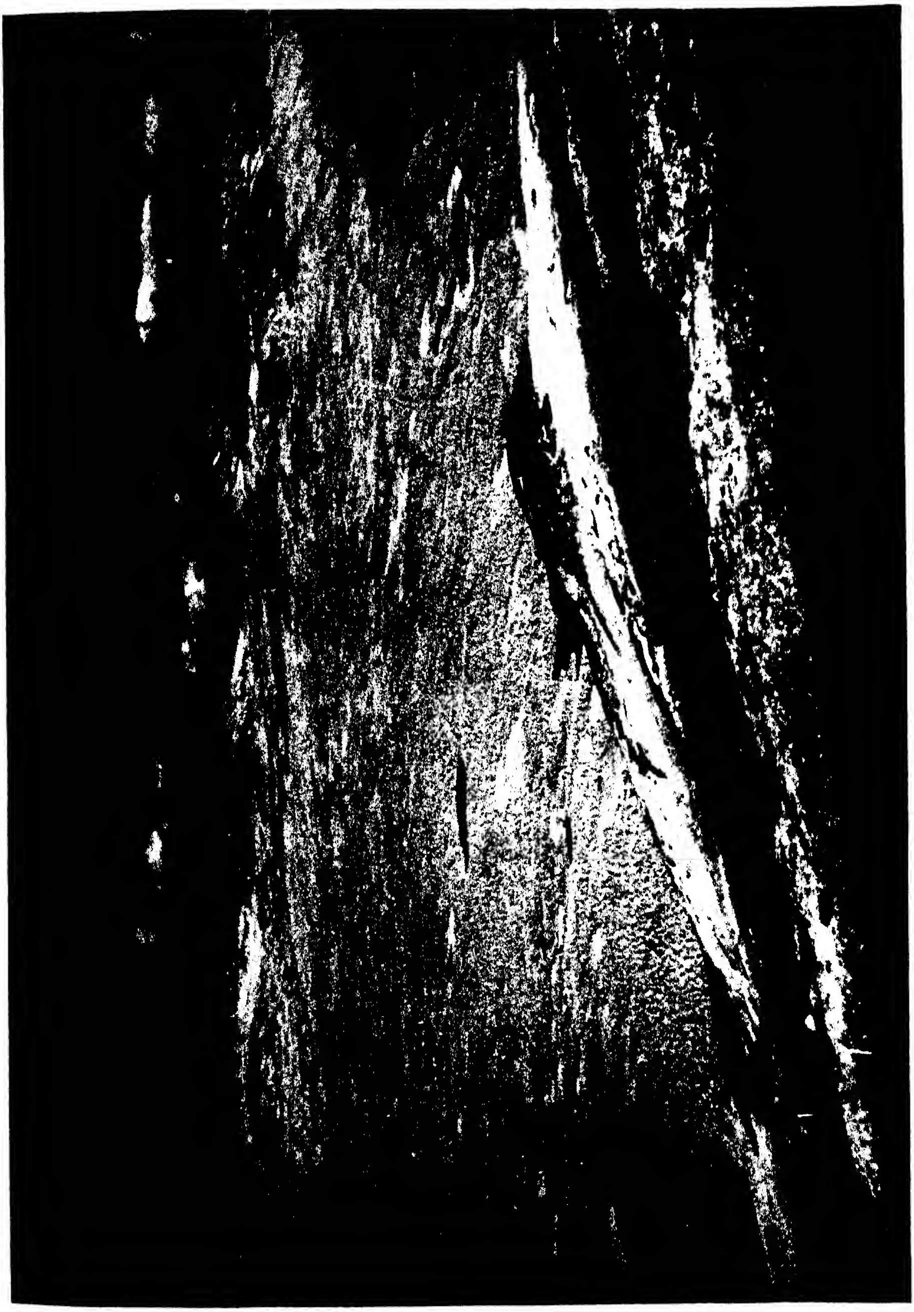
This photograph and note may serve to draw the attention of ecologists to the possibilities of infra-red photography in making a primary survey, though it is greatly desirable that the method should be tried out first upon other types of country, so that its exact limitations may be defined.

The illustration was taken at 6 p.m. (G.M.T.) on 13 July 1937 with the sun behind the photographer. The camera used was a Leica with Elmar lens stopped down to *f* 9, and the exposure given was ¼ sec.

Summary

1. A wide landscape in Arctic Lappland, photographed with infra-red sensitive material, gives sufficient tone contrast to distinguish the main vegetation areas.

2. It is recommended that ecologists should bear this method in mind for making rough primary surveys in a short time.



SOUTHERN and LEWIS—Infra-red Photograph of Arctic Birch Forest and Fells

Face p. 330

THE ROOTING SYSTEMS OF HEATH PLANTS

By G. H. HEATH and L. C. LUCKWILL

WITH A SECTION ON THE UNDERGROUND ORGANS OF HEATH BRYOPHYTES

By O. J. PULLEN

From the Department of Botany, The University, Bristol

(*With twelve Figures in the Text*)

CONTENTS

1. Introduction

Fritsch & Salisbury (1915) in their account of the vegetation of Hindhead Common give notes on the working and maximum depths of the rooting systems of the dominant plants. Other than these preliminary observations there appears to be no account of the underground organs of heath plants in the published literature, and the present investigation was undertaken in order to gain knowledge of this little-known though important aspect of the heath flora.

The observations were made on a stretch of heathland known as Blackdown, situated on the Mendip Hills in Somerset. A full account of the vegetation of Blackdown and of the ecological factors determining it are being published elsewhere, but a brief summary of the general ecology is given below. Special attention has been directed to those features which might be expected to influence, either directly or indirectly, the form of the rooting system.

2. General description of the area

The area in question is a slightly convex plateau, 2 km. in length and from 0·25 to 0·5 km. in width, situated at just over 300 m. above sea-level. The underlying rock is Old Red Sandstone.

The vegetation of the summit plateau is dominated by *Calluna vulgaris*. In this community *Erica tetralix* is abundant, and after firing it usually becomes codominant with *Calluna* and *Molinia* over large areas. *Erica cinerea* is of less frequent occurrence but is locally plentiful on the better drained parts of the heath, whilst the dwarf *Ulex Gallii* shows a somewhat localized distribution along the borders of paths and *Molinia* "flushes". On the damper parts of the heath *Molinia coerulea* replaces *Calluna* as the dominant plant and in such situations *Nardus stricta* is often subdominant. *Pteridium aquilinum* is the dominant plant on the flanks of the hill and is also present over a small area on the summit where it is accompanied by *Vaccinium Myrtillus* as codominant. The distribution within the area of these three principal plant communities would appear to be controlled by edaphic factors.

3. Edaphic conditions

The work of Weaver (1919) and others has shown that the form of the rooting system of a given species depends largely upon the prevailing edaphic conditions, so that any investigation of rooting systems, if it is to be of comparative value, should be accompanied by a survey of the edaphic factors. Such a survey was carried out on Blackdown in 1928–9, and the principal results are presented in the following account.

(*a*) *Soil profiles.* In all communities the soil profile shows three layers, viz. surface peat, subpeat, and stony layer. The surface peat is fibrous, almost black in colour when wet, and is covered with a layer of raw humus to a depth of $\frac{1}{2}$–1 cm. The subpeat is less fibrous in texture and contains sandy particles and stones. In regions where *Molinia* is dominant these two layers are not clearly differentiated, the subpeat being darkly stained with humus compounds washed down from the layer above. The stony layer beneath the subpeat is light brown in colour and consists of a heavy sandy loam containing many stones, which with increasing depth become larger and more numerous, until at a depth of about 12 or 15 cm. below the subpeat the underlying sandstone is reached. The depth of the surface peat varies from 2·5 cm. under *Pteridium*, to about 15 cm. under *Calluna*; that of the subpeat from 5·0 cm. under *Pteridium* to 22 cm. under *Calluna*.

Mechanical analysis shows that the subpeat consists of rather coarse particles which, however, become smaller with increasing depth. At 10 cm. 70 % of the particles were found to exceed 1 mm. in diameter, whilst at 15 cm. 50 % were below 0·5 mm. The sandy loam below the subpeat is composed of smaller particles which range from 0·12 to 0·03 mm. in diameter, 70 % being below 0·04 mm.

(*b*) *Water content, humus content, and acidity.* From an examination of Table I, which is a summary of the results of soil analyses carried out over a period of four months from November till February, it will be seen that the mean water and humus contents of the soils in the different communities run

in an approximately similar sequence, so that the mean coefficients of humidity (Crump, 1913) which give an estimate of the available soil water, show no very marked differences.

Table I. *Mean value of water and humus content, coefficient of humidity (= water/humus), and acidity* (pH) *of Blackdown soils taken from situations where the species named were dominant. Samples taken once a month from November till February* 1929. *Values expressed as percentage of oven dry weight*

Depth in cm. ...	4	15	23	Mean
Water content:				
Calluna	298·5	79·6	30·2	102·8
Calluna-Erica	229·9	72·9	29·6	110·8
Molinia	446·4	185·3	137·3	256·3
Pteridium	147·2	48·6	25·5	73·7
Humus content:				
Calluna	68·7	19·9	5·3	31·3
Calluna-Erica	66·3	20·6	6·2	31·0
Molinia	74·4	42·6	29·5	48·9
Pteridium	32·6	10·2	5·0	15·9
Coefficient of humidity:				
Calluna	4·6	4·4	5·6	4·9
Calluna-Erica	3·5	3·8	4·8	4·0
Molinia	6·1	5·1	3·3	4·8
Pteridium	4·6	5·0	5·5	5·0
*p*H:				
Calluna	4·2	4·6	5·3	4·7
Calluna-Erica	3·9	4·7	5·3	4·6
Molinia	3·9	4·1	4·6	4·2
Pteridium	4·6	5·4	6·3	5·4

The *Calluna* and *Calluna-Erica* soils are very similar, although, as the coefficients of humidity show, the latter tend to be somewhat drier than the former. The more open nature of the vegetation, allowing more rapid evaporation from the soil surface is probably responsible for this difference. In all soils except those from regions where *Molinia* is dominant the coefficient of humidity increases with increasing depth. This is partly and perhaps entirely due to the increasing percentage of small inorganic soil particles between the depths of 10 and 25 cm., which by retaining a certain amount of capillary water would increase the coefficient of humidity. Where *Molinia* is dominant the coefficient of humidity gradient is much steeper and is in the opposite direction. The exceptionally high water contents of the upper *Molinia* soils are attributable to the fact that this community develops in depressed areas where it receives surface drainage water from the surrounding heath.

The mean *p*H values vary from 3·9 to 6·3, the most acid soils being found beneath *Molinia*, the least acid beneath *Pteridium*. In all soils the surface peat was found to be the most acid, the acidity falling with increasing depth and showing a close correlation with the humus content of the soil.

(*c*) *Soil aeration.* In Table II are summarized the results of investigations of soil aeration carried out between January and April. The values for any

given type of soil show a considerable range, but in general the peats are found to have a higher air content than the more compact subpeats. This is especially noticeable in the soils from localities where *Calluna* is dominant. Beneath *Molinia* the high water content of the surface peat is responsible for the low aeration values. The surface peat beneath *Pteridium* was too thin to enable a large enough sample to be taken for the determination of the air content, but the subpeat shows comparatively high aeration values.

Table II. *Air contents as percentage by volume of Blackdown soils*

Type of vegetation	Surface peat	Subpeat	Stony layer
Calluna	10–20	2–8	—
Pteridium	—	17–30	—
Vaccinium	12–50	10–20	—
Molinia	4–6	7–11	1–4

4. Method of investigation

The following descriptions are based on the examination of from six to a dozen plants of each species, taken from localities where the plant was dominant or very abundant. In several instances where the plant was abundant in more than one community, marked variations were observed in the form of the rooting system, and the different types have been described separately. The method employed in the examination of the rooting system depended somewhat on the size of the plant. In the case of a fully grown *Ulex* bush the only way was to dig a trench alongside the plant and excavate the rooting system in the field. All the remaining species were dug up *in situ* and transferred to the laboratory where the roots were excavated with the aid of a strong jet of water. To facilitate the mapping of the rooting systems a piece of glass, marked with a diamond into 1 in. (2·54 cm.) squares, was used, which was placed over the specimen. In the case of the smaller species the drawings represent the complete rooting system, but in the case of the larger heaths where this was impracticable, bisects only of the system are represented.

The following abbreviations are used in the descriptions: W.D. = working depth; M.D. = maximum depth of penetration; L.S. = lateral spread. The drawings (except Fig. 2) are divided to represent 1 in. (= 2·54 cm.) squares.

5. Descriptions of rooting systems

(i) Polygala serpyllacea *Weihe*

Roots. White, fibrous; endotrophic mycorhiza in cortex; root hairs absent.

Rooting system. (*a*) Of plants growing amongst *Pteridium* (Fig. 1*b*) W.D. = 2·5–13·0 cm.; M.D. = 16·5 cm.; L.S. = 7–10 cm. A main root system with little lateral spread. Tap root only distinguishable in young plants. Upper laterals elongate rapidly, branch extensively, and soon equal or exceed the main root. They arise at an angle of 30 or 40 degrees to the main root but tend to grow downwards towards their extremities.

(*b*) Of plants growing amongst *Molinia* (Fig. 1*a*) W.D. = 2·5–6·5 cm.; M.D. = 10 cm.; L.S. = 15–20 cm. Roots stouter and less finely branched than in (*a*). Tap shorter and distinct from laterals which run horizontally for a considerable distance, giving the system a moderate amount of lateral spread.

(ii) Ulex Gallii *Planch*

Roots. Tap and laterals very stout, woody, 2·5–4 cm. in diameter at top; bacterial nodules but no mycorhizal associations; root hairs on finer rootlets.

Rooting system (Fig. 2). W.D. = 0–15 cm.; M.D. = 76 cm.; L.S. = 183 cm. A very extensive system with an exceptionally deep tap root. Laterals run for a metre or more a few centimetres below surface. Young plants with a well-developed tap and short, unbranched, horizontal laterals. Later laterals elongate rapidly and become finely branched at their extremities. Main root system supplemented by a fine mat of adventitious roots from the swollen bases of aerial stems.

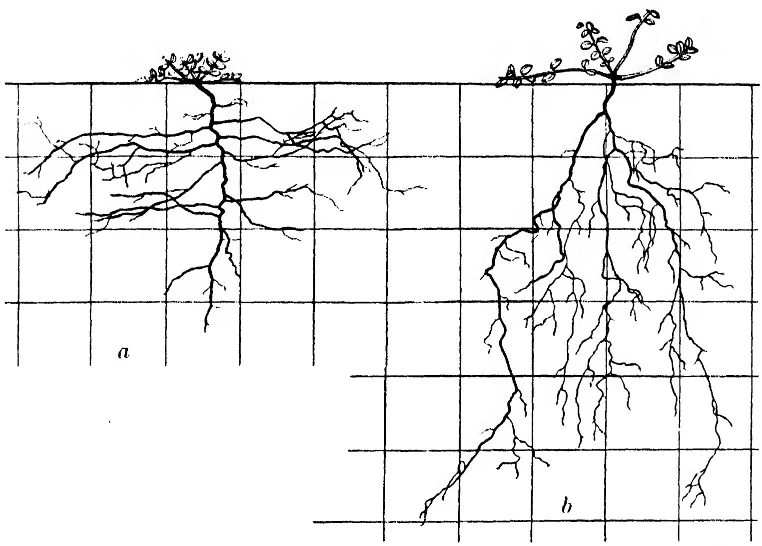


FIG. 1. *Polygala serpyllacea* Weihe. *a* = rooting system of a plant growing amongst *Molinia*, where the soil is waterlogged and acid; *b* = rooting system of a plant growing beneath *Pteridium* where the soil is better aerated and less acid.

(iii) Potentilla erecta *Hampe*

Rootstock. Tuberous, woody; situated just below the soil surface; roots and aerial shoots arise adventitiously from its surface.

Roots. (*a*) Of plants growing amongst young *Calluna* and *Erica tetralix* (Fig. 3*a*). Tap root when present poorly developed, unbranched, often becoming horizontal at a depth of 4 or 5 cm. Adventitious roots ½–2 mm. in

diameter, with a few short fibrous and almost unbranched laterals. White at first, later brown and suberized.

(*b*) Of plants growing amongst *Pteridium* (Fig. 3*b*). Tap root well developed, unbranched, woody, penetrating vertically. Adventitious roots as above but with longer and more finely branched rootlets.

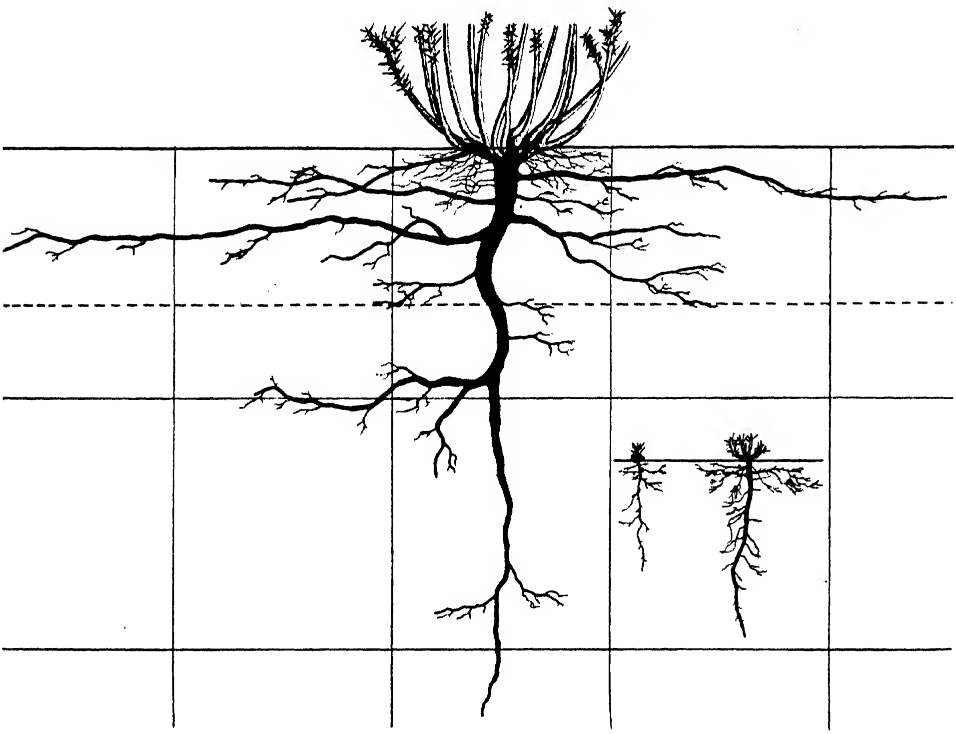


FIG. 2. *Ulex Gallii* Planch. Rooting system of a bush growing amongst *Calluna* on the border of a path where this plant is particularly abundant. The system was exposed by digging a trench alongside the plant. The lower limit of the subpeat is shown by the dotted line, beneath which is a heavy loam containing numerous large stones. The inset shows the rooting systems of young plants before the elongation of the upper laterals has set in. Each square = 30 × 30 cm.

Both types have mycorhiza in cortex of adventitious roots. Root hairs absent.

Rooting system. (*a*) W.D. = 1·5–6·5 cm.; M.D. = 10 cm.; L.S. = 10–12·5 cm. A shallow system with a moderate amount of lateral spread.

(*b*) W.D. = 2·5–7·5 cm.; M.D. = 15 cm.; L.S. = 10–12·5 cm. A deeper and more well-developed system.

(iv) Galium saxatile *L.*

Roots. White, fibrous; mycorhiza in primary and secondary roots and occasionally in those of higher order; root hairs occur sparingly on the finer rootlets.

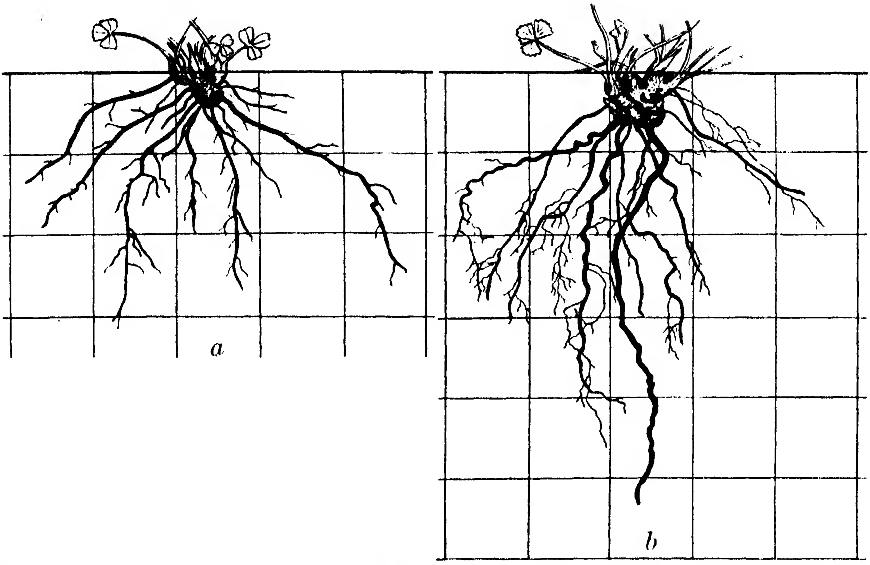


FIG. 3. *Potentilla erecta* Hampe. *a* = rooting system of a plant growing amongst young *Calluna*. Tap root absent. *b* = rooting system of a plant growing in the better aerated and less acid soil beneath *Pteridium*. Tap root long and unbranched.

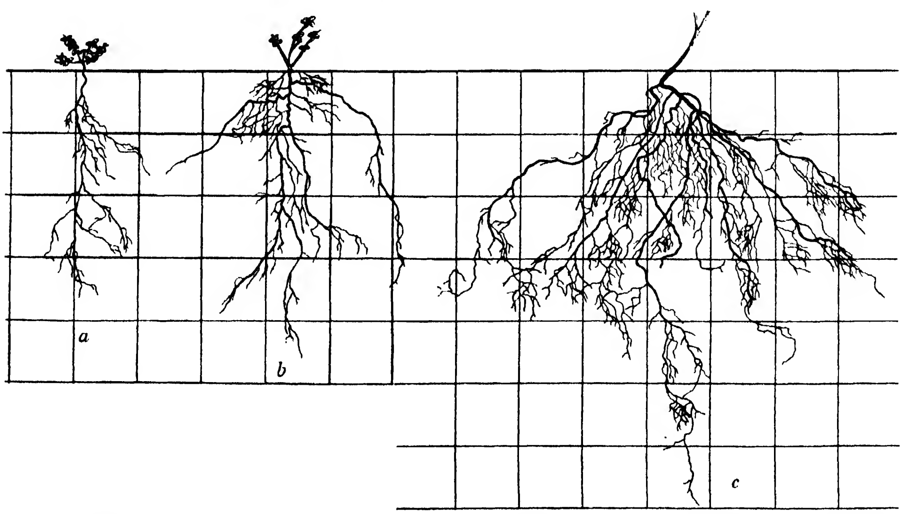


FIG. 4. *Galium saxatile* L. Rooting systems of plants of different ages growing beneath *Pteridium*. In *c* the primary root has become obscured by the strong growth of the upper laterals, the commencement of which can be seen in *b*.

Rooting system (Fig. 4). W.D. = 0·5–7·5 cm.; M.D. = 17·5 cm.; L.S. = 15–17 cm. A main root system; long strongly growing laterals with highly branched rootlets arise near soil surface and grow obliquely outwards; moderate lateral spread. Adventitious roots are occasionally developed from the lower nodes of the stem.

(v) Vaccinium Myrtillus *L.*

Rhizome. Very extensive; sympodial; 3–6 mm. in diameter; grows 6–25 mm. below soil surface; frequently branched, forming a close interlacing network; young rhizomes pink with brownish scale leaves; older rhizomes dark brown and suberized.

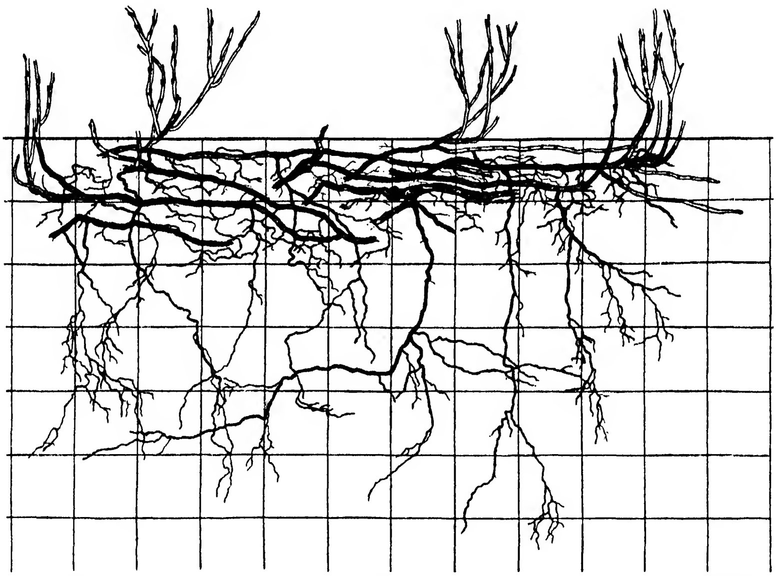


FIG. 5. *Vaccinium Myrtillus* L. Rooting systems of rhizomes growing amongst *Pteridium* in a region where the two plants were codominant.

Roots. Fibrous, much branched, and suberized early; maximum diameter 1·5–2 mm.; finer non-suberized rootlets with brown and colourless hyphae in outer cortex.

Rooting system (Fig. 5). W.D. = 2–13 cm.; M.D. = 17 cm. Entirely adventitious. The top 5 cm. of peat are occupied by a mat of short fine adventitious roots which ramify in all directions. The larger roots pursue a downward course and are much branched.

(vi) Erica tetralix *L.*

Rootstock (Fig. 6). Short, branched, prostrate, shallow; 1–1·5 cm. in diameter, arising from the hypocotyl region; aerial shoots from adventitious buds forming a small compact tussock.

Roots. White at first, later black; strongly suberized and woody; much branched; non-suberized rootlets infected with mycorhizal hyphae, especially those of the surface mat. Root hairs absent.

Rooting system (Fig. 7). W.D. = 0–7·5 cm.; M.D. = 18 cm. A shallow system with considerable lateral spread. Tap root obscured in old plants by strong growth of laterals. Largest laterals tend to grow horizontally in the top 5–8 cm. of soil, giving off secondary laterals which penetrate vertically. A surface mat of fine adventitious roots develops after the fourth year.

(vii) Erica cinerea *L.*

Rootstock. Less branched and more elongated than in *E. tetralix* or *Calluna*, growing upwards through raw humus and producing adventitious roots at successively higher levels.

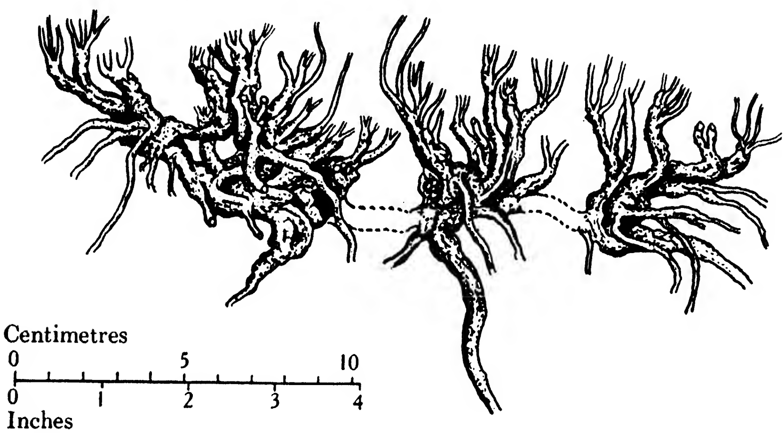


FIG. 6. *Erica tetralix* L. Rootstock of a twelve-year-old plant from which the finer roots have been removed, showing the creeping habit.

Roots. Stout, woody, often attaining a diameter of 1 cm.; lateral rootlets and adventitious roots fine, extensively branched, especially towards extremities; strong mycorhizal infection; root hairs absent.

Rooting system (Fig. 8). W.D. = 0–7·5 cm.; M.D. = 17·5 cm. Similar to that of *E. tetralix* but usually shallower. Top 5–8 cm. of soil very fully exploited by a well-developed surface mat. Tap root decays after about eight years.

(viii) Calluna vulgaris *Salisb.*

Rootstock. As in *Erica tetralix*, but stouter, less branched, and somewhat more deeply buried.

Roots. Main and primary lateral roots 0·5–1 cm. in diameter; extensively suberized after the first year; finer non-suberized roots with brown and colourless hyphae in outer cortex; root hairs absent.

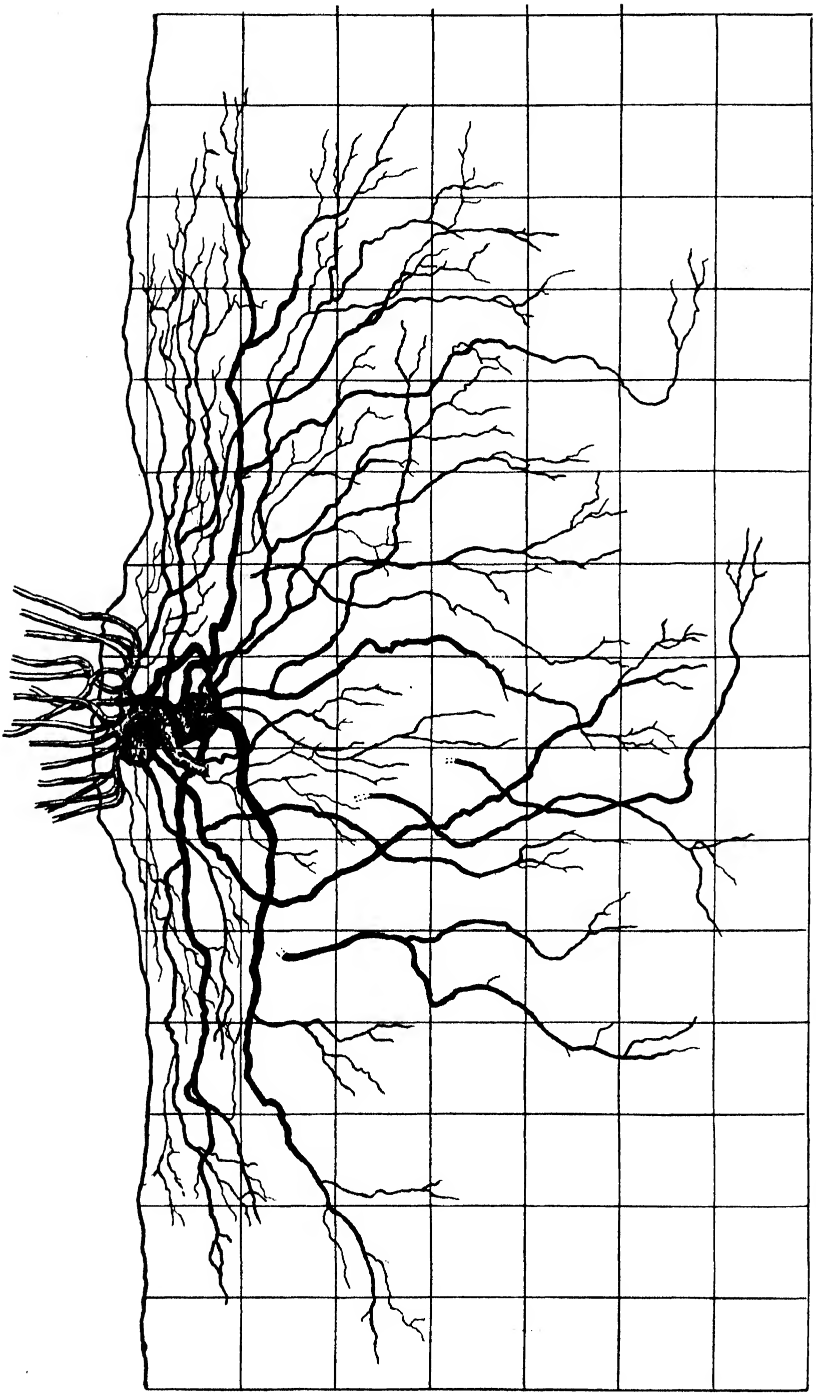


FIG. 7. *Erica tetralix* L. Bisect of the rooting system of a small tussock, 14–15 years old, growing amongst *Calluna*. In this particular specimen the primary root has become horizontal at depth of about 3 cm.

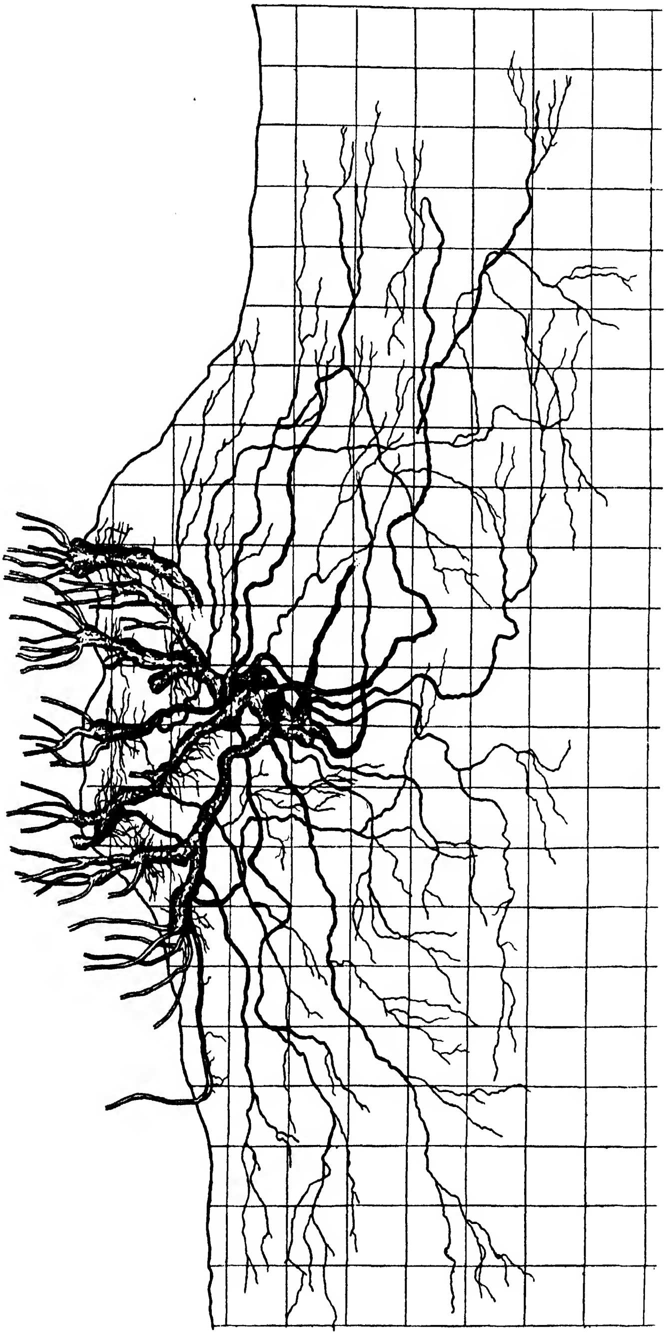


FIG. 8. *Erica cinerea* L. Bisect of the rooting system of a large plant, about 19 years old, growing in a situation where this plant is locally dominant. The soils in such regions have a considerably lower humus and water content than typical *Calluna* soils and a slightly lower acidity. Note the elongated rootstock with fine adventitious rootlets.

Rooting system (Fig. 9). W.D. = 0–10 cm.; M.D. = 23 cm. Young plants with a well-marked tap root which is later obscured by stronger growth and branching of laterals. Roots in top 5–8 cm. of soil tend to run horizontally. At lower depths they are more or less vertical. Top 5 cm. of soil occupied by surface mat formed of adventitious roots and finer branches of main root system.

(ix) Pedicularis sylvatica *L.*

Roots. Short, white, fleshy, very brittle, with a wrinkled surface; feebly branched; no signs of parasitic attachment were observed.

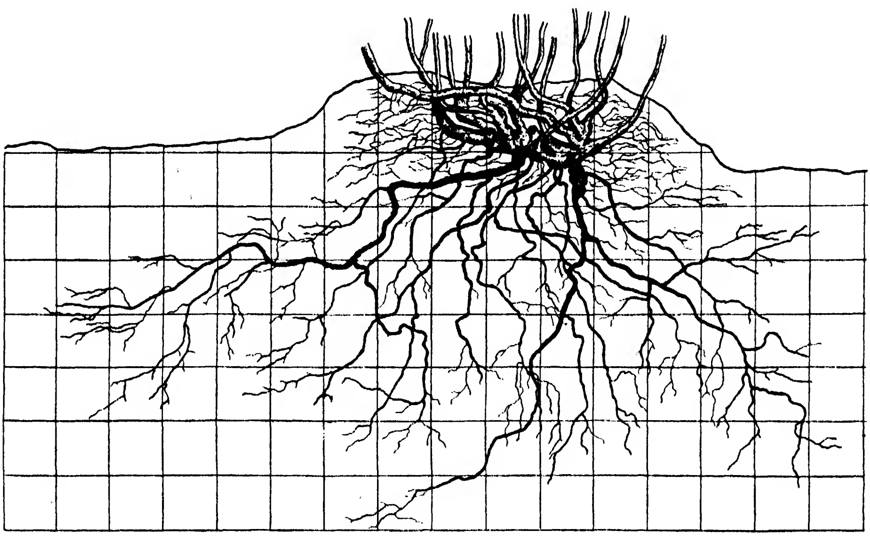


FIG. 9. *Calluna vulgaris* Salisb. Bisect of the rooting system of a 12-year-old plant. Note the well-developed surface mat of adventitious rootlets.

Rooting system. W.D. = 2·5–7·5 cm.; M.D. = 9 cm. Very poorly developed as is characteristic of the partial parasites. Tap root carrot shaped with a few short, stout, almost unbranched laterals arising at an angle of about 45°.

(x) Narthecium ossifragum *Huds.*

Rhizome. Pale yellow, occasionally branched, 3–5 mm. in diameter; its growth is sympodial or monopodial according to whether a flowering stalk is produced or not. Geotropic reaction of the rhizome appears to vary from plant to plant; some grow vertically in the *Sphagnum*, others horizontally.

Roots. Of two types: (*a*) Long cord roots, 1–2 mm. in diameter, almost devoid of lateral roots. These are most abundant near the apex of the rhizome. (*b*) Shorter fibrous roots with many finely branched rootlets. Endotrophic mycorhiza in cortex; root hairs absent.

Rooting system. (*a*) Horizontal rhizomes (Fig. 10*b*). W.D. = 2–10 cm.; M.D. = 25 cm. Cord roots penetrate vertically for 20 cm. or more; fibrous roots, 5–10 cm. long, grow out at an angle of about 45°.

(*b*) Vertical rhizomes (Fig. 10*a*). W.D. = 2–10 cm.; M.D. indeterminate. All roots grow horizontally in the upper 10 cm. of soil. Cord roots shorter and less well developed than in (*a*).

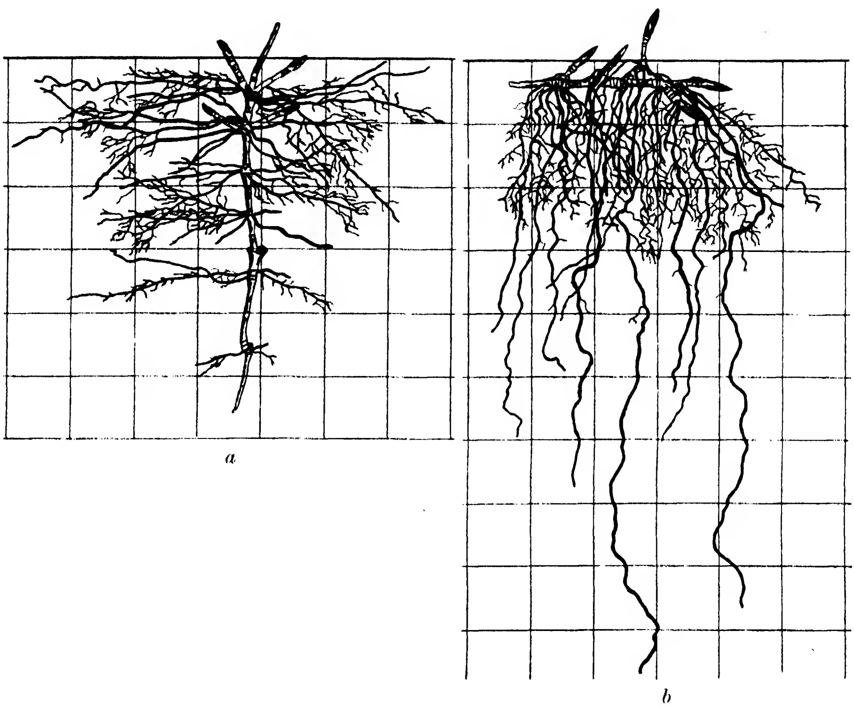


FIG. 10. *Narthecium ossifragum* Huds. Rooting systems of rhizomes growing in loose *Sphagnum* peat. *a* = vertical type of rhizome; *b* = horizontal type of rhizome (see text).

(xi) Juncus squarrosus *L.*

Rhizome. Branched, sympodial, 6–12 mm. in diameter, growing horizontally at a depth of about 2 cm.; concealed by a dense covering of old leaf bases.

Roots. Cord root type; long, unbranched, light brown, with a wrinkled surface; 2–3 mm. in diameter when mature; short lateral rootlets occur sparingly on the younger cord roots; root hairs 1–3 mm. long, forming a dense weft around the root.

Rooting system (Fig. 11). W.D. = 2·5–9 cm.; M.D. = 27 cm. All roots tend to grow vertically downwards. Little lateral spread. Most roots are within the top 10 cm. of soil, and only a few of the cord roots penetrate deeply.

(xii) Scirpus caespitosus *L.*

Rhizome. Light brown, sympodially branched, 2–3 mm. in diameter, growing vertically in the peat; new rhizome grows upwards within the leaf bases and scale leaves of preceding years, and adventitious roots grow downwards under cover of old leaf bases for 4 or 5 cm. before entering soil. Continual branching of the vertical rhizome gives compact tussock formation.

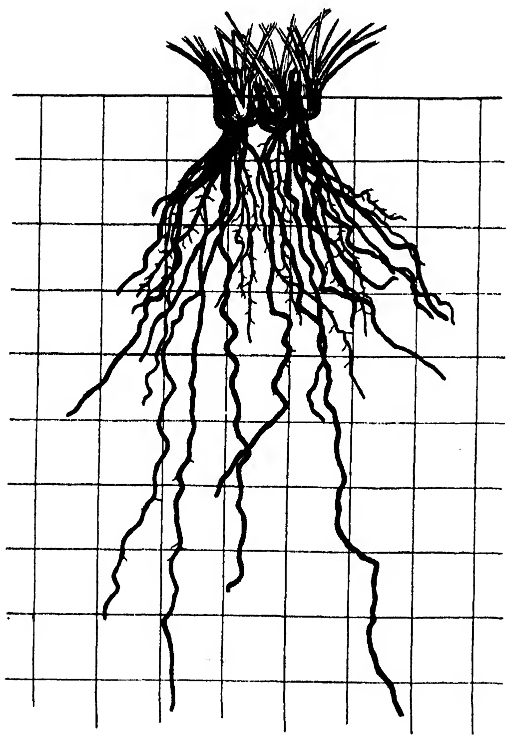


FIG. 11. *Juncus squarrosus* L. Growing amongst *Calluna* and *Molinia*. Rooting system of a small portion of a tussock formed by the branching of the rhizome. Most of the rhizome, which was about 17 cm. long, has been removed. Typical monocot. type.

Roots. Cord root type, 1–1·5 mm. in diameter, with numerous short laterals; root hairs occur sparingly on cord and lateral roots; mycorhiza in cortex of laterals.

Rooting system. W.D. = 0–15 cm.; M.D. = 25 cm. A vertical system with no marked lateral spread. Owing to the very close growth of the rhizomes there is a dense tangled mass of roots in the top 12 cm. of soil. Few roots penetrate beyond a depth of 18 cm.

(xiii) Carex binervis *Sm.*

Rhizome. Horizontal, 2·5–4 cm. below surface; light brown, sympodial, frequently branched; about 6 mm. in diameter.

Roots. Cord root type; 1–2 mm. in diameter, with short lateral rootlets; root hairs occur chiefly on the lateral rootlets.

Rooting system. W.D. = 2·5–15 cm.; M.D. = 18 cm. Similar to that of *Juncus squarrosus* but shallower and with more lateral spread.

(xiv) Molinia coerulea *Moench.*

Rhizome. Short, compact, much branched, forming a close tussock; white; about 6 mm. in diameter and covered with peg-like leaf bases from the axils of which the cord roots arise.

Roots. Of two types: (*a*) Cord roots; long, white, 1 mm. in diameter throughout length; devoid of root hairs.

(*b*) Fibrous roots; these arise from the cord roots and are fine, much branched and have abundant root hairs. Both types of root have cortical mycorhiza.

Rooting system. W.D. = 2·5–20 cm.; M.D. = 33 cm. A very deep system with little lateral spread. Cord roots penetrate vertically giving off fibrous roots at intervals along their length, which ramify in all directions.

(xv) Nardus stricta *L.*

Rhizome. Sympodial, about 1 cm. in diameter and densely covered with old leaf bases; grows horizontally at a depth of 2–5 cm. and may attain a third of a metre or more in length; frequently branched.

Roots. Cord and fibrous roots as in *Molinia*. Mycorhiza occurs chiefly in the fibrous roots.

Rooting system. W.D. = 2–15 cm.; M.D. = 28 cm. Very similar to that of *Molinia* but somewhat shallower and less profusely branched.

(xvi) Pteridium aquilinum *L.*

Rhizome. Black; 0·6–2 cm. in diameter; frequently branched; grows horizontally at a depth of 9–18 cm. The branches of the rhizome become separated from one another by the decay of the older portions.

Roots. Stout; black; wiry.

Rooting system. W.D. = 7·5–15 cm.; M.D. = 22 cm. Most of the roots spring from near the apex of the rhizome, i.e. near the base of this year's leaf stalk, and only a few persist on the older parts. They are usually quite short, with few laterals, and ramify in all directions. The paucity of the rooting system is compensated for by the extensive spread of the rhizomes.

6. Classification of rooting systems

The rooting systems of the species examined (with the exception of that of *Pteridium*) belong to one of three main ecological types. These are:

Type 1. Comparatively shallow systems with a considerable lateral spread. The working region of the systems extends from the soil surface to a depth of about 10 cm., and the maximum depth is usually about 20 cm. The surface layers of soil are exploited by a mat of fine adventitious rootlets, e.g. *Calluna vulgaris*, *Erica tetralix*, *E. cinerea*, *Vaccinium Myrtillus*, *Ulex Gallii*.

Type 2. Small systems whose working depth lies approximately between the depths of 2 and 8 cm. with a maximum depth of 10 to 15 cm. depending on the type of soil. Few absorbing rootlets produced in the surface layers of peat, e.g. *Galium saxatile*, *Polygala serpyllacea*, *Potentilla erecta*, *Pedicularis sylvatica*.

Type 3 (monocot. type). Deep systems with little lateral spread. The working depth usually extends from a depth of 2 cm. to 10 or 15 cm. and the maximum depth is about 30 cm. This type includes all the monocotyledonous members of the heath flora. The uppermost 2–3 cm. of soil are occupied by the closely growing rhizomes, which often branch extensively to give compact tussocks.

Root competition tends to be greatest amongst plants which have rooting systems which are ecologically similar, that is, between plants belonging to the same type in the above classification.

In communities dominated by *Calluna* and also in those dominated by *Molinia*, the rooting systems of the most abundant plants are of the same type and root competition in these communities is probably a factor of importance. In *Calluna* communities it may be the factor which prevents the closer growth of the ericaceous shrubs, for even after a fire, which destroys the aerial parts of the plants but does not kill the underground organs, seedlings of *Calluna* and *Erica* spp. fail to establish themselves for long on the bare areas of peat between the shrubs. In the *Molinia* grassland the plants are enabled to grow in close proximity because their rooting systems have very little lateral spread, and in *Pteridium* communities the close growth of the individual plants is made possible by the fact that their rooting systems are of different ecological types, i.e. there is a stratification of the underground organs.

7. General observations

(*a*) *Ecological relations*

The comparative rooting depths of plants in the different communities studied, together with the corresponding depths of surface peat and subpeat, can be seen from the accompanying table (Table III). There appears to be a definite correlation between the form of the rooting system and the prevailing edaphic conditions. In communities dominated by *Calluna* the working regions of the rooting systems lie within the comparatively well-aerated surface peat

and very few absorbing roots are developed in the poorly aerated though less acid subpeat. In communities in which *Pteridium* is dominant the absorbing zone tends to lie somewhat deeper and is here situated in the well-aerated subpeat and upper region of the stony layer. The roots of the plants growing in this community tend to be more fibrous and more highly branched than those of plants from regions dominated by *Calluna* or *Molinia*, a phenomenon which again would appear to be correlated with the better aeration of the soil (see Figs. 1 and 3). Where *Molinia* is dominant the plants have rooting systems which penetrate comparatively deeply, but the absorbing region lies chiefly in the subpeat and lower layers of surface peat.

Table III. *Comparative rooting depths of heath plants growing in different communities together with the corresponding average depth of surface peat and subpeat.* W.D. = *working depth (the upper and lower limits are given)*; M.D. = *maximum depth of penetration. All measurements are in cm.*

Dominant plant in community	Peat depth: Surface	Peat depth: Subpeat	Species	W.D.	M.D.
Calluna	15	20	*Calluna vulgaris*	0·0–10·0	23·0
			Erica tetralix	0·0– 7·5	18·0
			E. cinerea	0·0– 7·5	17·5
			Potentilla erecta	1·5– 6·5	10·0
			Ulex Gallii	0·0–15·0	76·0
			Juncus squarrosus	2·5– 9·0	27·0
			Pedicularis sylvatica	2·5– 7·5	9·0
Pteridium	2	5	*Pteridium aquilinum*	7·5–15·0	22·0
			Vaccinium Myrtillus	2·0–13·0	17·0
			Potentilla erecta	2·5– 7·5	15·0
			Carex binervis	2·5–15·0	18·0
			Polygala serpyllacea	2·5–13·0	16·5
			Galium saxatile	0·5– 7·5	17·5
Molinia	8	15	*Molinia coerulea*	2·5–20·0	33·0
			Nardus stricta	2·5–15·0	28·0
			Scirpus caespitosus	0·0–15·0	25·0
			Polygala serpyllacea	2·5– 6·5	10·0
Sphagnum	—	—	*Narthecium ossifragum*	2·0–10·0	25·0

(b) *Anatomical characteristics*

An anatomical investigation was made of the roots of all the species described above but there appeared to be no special anatomical features common to all.

The development of cortical air cavities is most frequent in the monocotyledonous members of the heath flora which are characteristic of poorly aerated soils. There are however many exceptions, e.g. *Carex binervis* with well-developed air cavities is a characteristic plant of the well-aerated soil beneath *Pteridium*, whereas *Molinia* growing in wet soil has few.

The conducting tissue of the root usually shows a normal development, although three species, viz. *Ulex Gallii*, *Potentilla erecta*, and *Pedicularis sylvatica* show a very poor development of secondary xylem. The development of a corky covering on all but the youngest roots is a feature characteristic of

those plants which grow in the drier fibrous peat of regions dominated by *Calluna*, e.g. *Calluna vulgaris*, *Erica tetralix*, *E. cinerea*, *Vaccinium Myrtillus*, *Potentilla erecta*, *Ulex Gallii*, and is possibly related, either as cause or effect, to the high suction force which a soil of such high humus content would exert when it began to dry out. Maximov (1929) has put forward a similar explanation to account for the same phenomenon in the roots of desert plants.

Endotrophic mycorhiza is of very common occurrence in the roots of heath plants and was present in 12 out of 16 species examined. Root hairs are frequently not developed when a mycorhiza is present, but at least four of the species examined had both root hairs and mycorhiza, viz. *Galium saxatile* *Nardus stricta*, *Molinia coerulea*, *Scirpus caespitosus*.

(*c*) *Reduction of the main root system*

It is possible to arrange the rooting systems of the plants examined in a rough series showing a progressive reduction of the main root system in favour of an adventitious system developed on an extensive rhizome. Such a series extends from types such as *Polygala*, which possess a typical main root system with tap and laterals, to *Vaccinium*, in which a tap root is present only in the seedling stage and the whole root system of the adult plant is adventitious. The following plants are examples of different stages in this reduction:

(1) *Polygala*. Main root system.

(2) *Galium*. Main root system. Adventitious roots occasionally developed from lower nodes of stem.

(3) *Ulex*. Main root system supplemented by adventitious roots developed from buried bases of aerial stems.

(4) *Calluna* and *Erica tetralix*. Similar to that of *Ulex* but aerial shoots arise from adventitious buds on short branched rootstocks. Surface mat of adventitious roots more fully developed.

(5) *Erica cinerea*. Extensive system of adventitious roots developed from rootstock which is somewhat more elongated than in *E. tetralix*. Tap root becomes brittle and dies away after about eight years.

(6) *Potentilla*. Main root system is reduced to a woody unbranched, and apparently functionless tap root. Absorption is carried on only by stout adventitious roots developed from a swollen underground stem.

(7) *Vaccinium* (also *Carex*, *Juncus*, and the heath grasses). Main root system does not persist after the seedling stage. Adventitious root system developed from more or less extensive rhizomes.

It is easy to understand why the development of adventitious roots is such a prevalent feature amongst heath plants. Humus is continually collecting underneath the plants and becoming converted into peat, so that the bases of the aerial stems become buried, and as a consequence develop roots adventitiously from their surface. Further development along these lines would result

in rhizomes, at first short as in *Calluna* and later long and creeping as in *Vaccinium*, bearing roots on their surface. Regarding the biological advantage to the plant of replacing the main root system by such an adventitiously developed system, it may be pointed out that adventitious roots from the buried bases of aerial stems are necessarily formed near the surface, where the soil is comparatively well aerated and more favourable to root development than at lower levels. This would at once confer an advantage on such a system. Moreover the development of elongated rhizomes, besides offering a ready means of vegetative propagation, would be of advantage in enabling the plant to exploit a larger volume of surface soil than would otherwise be possible.

These speculations apply chiefly to the dicotyledons of the heath flora. In the case of the monocotyledonous members the converse relationship probably holds, namely, that instead of developing adventitious roots in response to the peat habitat, they occupy the peat habitat because they happen to possess rooting systems which are suited to it.

8. THE UNDERGROUND SYSTEMS OF CERTAIN BRYOPHYTES

The underground organs of certain bryophytes characteristic of the heath communities on Blackdown were investigated and were found to belong to one of three types, viz.:

(1) Species of *Polytrichum* with extensive rhizome systems. *P. commune*, *P. juniperinum*.

(2) A group of larger mosses which, after preliminary attachment to the soil, form large cushions, the lower parts decaying. *Sphagnum* spp., *Hypnum cupressiforme*, *H. Schreberi*, *Dicranum scoparium*, *Aulacomnium palustre*.

(3) A group of small mosses closely attached to the peat and forming a compact mass of rhizoids and soil. *Campylopus flexuosus*, *Webera nutans*, *Ditrichum flexicaule*, *Bryum alpinum*.

Group 1

Polytrichum commune L. This plant has a very extensive system of branching rhizomes, bearing a dense mat of white rhizoids. Young plants show clearly the nature of the branching habit, but it appears that in older plants the upright branches become separated from each other by the decay of the older parts of the rhizome. Such old plants, which may attain a length of 30 cm. or more, occur in tufts, each plant of which consists of a single vertical axis springing from a short length of rhizome. The upper half of this axis is usually covered with green leaves and below this comes a zone of brown stem bearing the remains of leaves. This region of the stem is surrounded by loose fibrous peat and on sectioning reveals the anatomy described by Tansley & Chick (1901) as aerial stem. The lowermost region, usually about 5 cm. long, is covered with rhizoids and shows the true rhizome anatomy on sectioning.

Certain variations in the life form, correlated with changes in the nature and in the depth of the peat, may be observed on different parts of the heath.

In the *Molinia* grassland, *Polytrichum* shows about 15 cm. above the soil. In the upper 12 cm. of dark peat masses of rhizomes may be seen, whilst below this to a depth of about 30 cm. there are many traces of decaying branches.

In the *Sphagnum* bogs *Polytrichum* grows luxuriantly. The living portions of the plants are often 30 cm. or more in length, whilst the decaying remains of rhizomes are found to a depth of 1 m.

In regions where *Calluna* is dominant *Polytrichum* occurs in characteristic "pockets", which are small damp hollows in the ground. The peat is here shallow and beneath it is a layer of stones. The rhizomes form a mat at a depth of 5–8 cm. from which large numbers of upright shoots arise. There appears to be an entanglement or interlocking of the rhizomes of different plants forming peculiar knobs, the exact nature of which it is difficult to work out. On dissection these knobs are found to consist of a tight mass of rhizomes, rhizoids and clay.

Polytrichum juniperinum Willd. is common wherever the soil is comparatively well aerated, e.g. around rabbit burrows and on *Vaccinium* "hummocks". The underground organs of this species resemble those of *Polytrichum commune* under similar conditions.

The extensive underground system of *Polytrichum* is interesting because of its remarkable resemblance to that of an angiosperm. It may help to explain the success of this moss in competition with phanerogamic rivals, since when the aerial shoots are destroyed by fire, new shoots can arise from any part of the rhizome. It is evident from the considerable depths at which the remains of this moss are found, that it has been growing in the areas mentioned for a very long time.

Group 2

Hypnum cupressiforme L. This moss is commonly found forming cushions around the bases of plants of *Calluna* from 8 to 10 years of age. The base of the cushion was always found to be so far decayed that, in spite of careful dissection, it was not possible to see the original connexion between plant and soil. Water appears to be absorbed by the whole plant, and rhizoids are only occasionally produced. Each cushion is made up of many individuals and their branched axes straggle along the soil surface, all lying in the same direction. The cushions are remarkably drought resistant. When air-dried in the laboratory the leaves remain quite green and recover immediately when water again becomes available. The variety *ericetorum* B. & S. forms similar cushions.

Hypnum Schreberi Willd. The habit of this moss is very similar to that of *H. cupressiforme* except that in the cushions the individuals lie in different directions. At certain points the plants are securely fixed to the peat by rhizoids, but in this moss also no primary attachments have been observed

It seems, therefore, that in the various species of *Hypnum*, the primary attachment is lost very early in the life of the individual.

Dicranum scoparium Hedw. This moss, which is most frequent on Blackdown amongst *Vaccinium* and "poor *Calluna*" (Fritsch & Salisbury, 1915), forms tall compact cushions. The primary attachment is strong and persists for 4 or 5 years; it occupies the uppermost 1 cm. of peat (Fig. 12). When it dies and decays, attachment is lost, and the individuals of the cushion rely only on the surrounding vegetation for support. The upright stems are occasionally branched and are covered with rhizoid-like organs which probably play a greater part in support than in the absorption of water.

Aulacomnium palustre Schwaeg. This moss forms large cushions in the *Sphagnum* bogs and in the *Molinia* grassland. The green stems can be traced

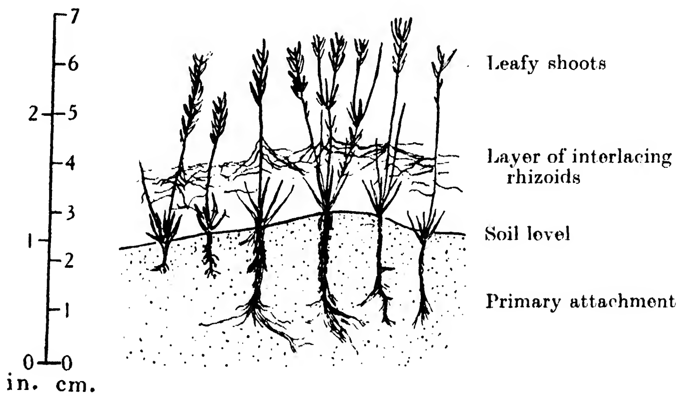


FIG. 12. *Dicranum scoparium* Hedw. Diagrammatic vertical section through cushion, showing the "rooting system".

downwards to masses of decaying stems and leaves in the peat beneath. The lower portions of these upright axes are much entangled, and appear as dark brown masses in the cushions.

Group 3

These small mosses possess no special underground systems. They are attached to the peat by large numbers of rhizoids and the connexion between peat and rhizoids is so intimate that they cannot be separated even by dissection or maceration.

9. SUMMARY

The observations were made on a stretch of Upland Heath in Somerset, three principal plant communities being represented on the area. These were dominated by *Calluna vulgaris*, *Molinia coerulea*, and *Pteridium aquilinum* respectively.

A study was made of the rooting systems of the most abundant plants in each of these three communities and their principal features are discussed in relation to the edaphic conditions. Altogether seventeen species were investigated and their rooting systems (with the exception of that of *Pteridium*) were found to belong to one of three main types. These were:

(1) Shallow systems with considerable lateral spread. Many absorbing rootlets in surface layers of soil.

(2) Small systems with no marked lateral spread. Few absorbing rootlets in surface layers of soil.

(3) Deep systems with little lateral spread (monocot. type).

It is considered that the peat habitat favours the replacement of a main root system with tap and laterals by an adventitious system developed on an elongated rhizome. The species investigated can be arranged in a series showing progressive stages in such a reduction.

The underground systems of various heath bryophytes are briefly described, three main types being distinguished. That of *Polytrichum* is especially interesting because of its remarkable resemblance to that of an angiosperm.

10. Acknowledgements

The writers wish to acknowledge their indebtedness to Dr R. Bracher, at whose suggestion the work was carried out, for her constant help and advice; to Prof. Macgregor Skene for his criticism of the manuscript, and to the late Sir Vernon Wills, the former owner of Blackdown, for his permission to carry out the survey. They also wish to thank the Colston Research Society for a grant in aid of publication.

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A PRELIMINARY STUDY OF THE PHYTOPLANKTON IN LAKE SARAH (NEW ZEALAND)

By E. A. FLINT

(*With one Figure in the Text*)

The periodicity of fresh-water algae has not so far been investigated in New Zealand, and the phytoplankton of Lake Sarah was chosen for study because the lake was conveniently situated about one mile from the Mountain Biological Station belonging to Canterbury University College.

The lake lies in a glaciated valley, 1870 ft. above sea-level, in the Cass district, which is located in the eastern foothills of the Southern Alps. The surrounding country is rugged and uncultivated, the smooth slopes bearing tussock and some scrub vegetation. The climate is typically subalpine, hot and dry in summer and cold and wet in winter. The rainfall is about 45 in. per annum, but no other meteorological data are available.

There are three lakes in the Cass district. Lake Sarah, the smallest, is separated on the south side, from Lake Grasmere by a low ridge of tussock land. On the east side it is bounded by a terminal moraine, on the north by an ancient shingle fan, and on the west by the swamp, out of which flows the Grasmere stream (Speight, 1916). The lake is about half a mile long and a quarter of a mile wide, with a maximum depth of 22 ft.; the seasonal variation in level is about 1 ft.

The distribution of the macrophytes on the floor of the lake apparently depends on the type of the substratum rather than on the depth of the water (cf. Pearsall, 1932). *Isoetes* grows in the crevices of a rocky substratum in shallow water, while *Chara* and *Nitella* are restricted to silt in deeper water (*Chara* in 6–10 ft., and *Nitella* in 8–18 ft.). Between these extreme types of habitat there is an intermediate one where the silt is very thin and is occupied by *Bulbochaete* sp. *Elodea canadensis* is confined to silt at a depth of 15 ft. or more, although in the Grasmere stream it is found in very shallow water wherever the silt is deep enough. Depth of water is, therefore, not a limiting factor.

Collections were made from the end of a 12 ft. jetty which was built out into the lake. The samples of plankton were taken by pouring a known volume (103 l.) of lake water through a small tow net (6 in. in diameter and 18 in. long), made of bolting silk with 157 meshes to the linear inch. The concentrated suspension obtained was measured and preserved in 2½ % formaldehyde. These samples were used both for qualitative and quantitative analyses.

The temperature of the water was determined at the jetty at the times of collection. The *p*H was estimated at the jetty with a Hellige comparator and

coloured glass standards. Readings of temperature and *p*H were made at ten other stations on the lake and showed only slight variation. The oxygen content of the water was estimated by Winkler's method (Kenwood, 1920).

The readings for temperature, *p*H and oxygen content are given in Fig. 1. There are no striking fluctuations, except the sudden fall in oxygen content in the winter (July 1935). A similar fall was observed in July 1934 and appears to be related to the paucity of phytoplankton. The apparent correlation between temperature and *p*H is noteworthy.

A Secchi disk was found to be visible at all depths and, if the degree of transparency be an index to the quantity of suspended matter in the water, then that quantity in Lake Sarah must be very small.

The values for total solids, P_2O_5, NO_3 and SiO_2 in Lake Sarah, given in the following table, were supplied by an analytical chemist. All values are expressed as parts per 100,000.

1934	P_2O_5	NO_3	SiO_2	Total solids	N/P ratio
April	0·050	0·00090	—	6·1	0·020
May	0·020	0·00085	—	5·3	0·050
July	0·083	0·00100	0·455	5·7	0·010
September	0·110	0·00100	0·135	4·8	0·009

A comparison of these figures with those given by Pearsall (1932) for the English lakes is of interest. In Lake Sarah the P_2O_5 content varies from 0·02 to 0·11; the NO_3 content from 0·00085 to 0·001, and the total solids average 5·4. In the English lakes the P_2O_5 content varies between 0·0003 and 0·018; the NO_3 content between 0·0005 and 0·02, and the total solids average 4·5. Lake Sarah is therefore characterized by a higher content in phosphate and total solids, but a lower content in nitrates than the English lakes. The waters of the lake are clearly oligotrophic in character and this is supported by the prominence of desmids in the plankton.

A low N/P ratio and low total solids have been correlated in the English lakes with a rich desmid flora and the same relationship holds for Lake Sarah. W. and G. S. West (1909) further showed that in Britain a desmid flora is typical of lakes on carboniferous or older rocks, but Lake Sarah, with a fairly rich desmid flora, is situated on Trias-Jura rocks.

In the following list of algae found in the plankton of Lake Sarah, the species are arranged according to their degree of importance.[1]

(*a*) Species *dominant* at some time during the year:

Asterionella gracillima (Hantzsch.) Heib., dominant during the spring months (September to November) but always represented in the plankton.

Botryococcus Braunii Kütz., dominant during summer and autumn (December to May) and found in all collections.

Volvox aureus Ehrenb., dominant in winter (June). From November 1935 to February 1936 it was present in all the samples.

[1] The writer is indebted to Dr H. Skuja who identified most of these species.

Epithemia sorex Kütz., dominant in July and present in all collections except that of April 1934.

Pandorina morum (Müll.) Bory, dominant in August and present in all samples.

Kirchneriella lunaris Moeb., dominant in February and represented mainly in the summer months.

(*b*) *Constant* species (as defined by Pearsall, 1932):

Eudorina elegans Ehrenb.
Bulbochaete sp.
Mougeotia sp.
Gonatozygon monotaenium De Bary
Cosmarium moniliforme (Turp.) Ralfs
 var. panduriformis West
C. contractum Kirchn.
Staurastrum lunatum Ralfs
S. avicula Bréb. var. subarctuum West
S. Manfeldtii Delp. var. annulatum West
S. tohopekaligense Wolle var. trifurcatum West
Tabellaria flocculosa (Roth) Kütz.
Cocconeis placentula (Ehrenb.)
Diatoma elongatum Agardh
Cymbella spp.
Synedra spp.
Gomphonema spp.
Aphanocapsa elachista West
Oscillatoria spp.
Anabaena sp.
Gomphosphaeria spp.

None of these species were ever dominant in the plankton. They were least represented in the winter although they varied in the degree of abundance in the two winters in which collections were made.

(*c*) Species which occurred in less than three-quarters of the samples (except *Dinobryon sertularia*, usually rare in the plankton):

Gonium pectorale Müll.
Sphaerocystis Schroeteri Chod.
Gleocystis planctonica (W. & G. S. West) Lemm.
Oocystis Borgei Snow
O. solitaria Wittr.
O. solitaria var. apiculata Printz.
Nephrocytium lunatum W. West
Dictyosphaerium Ehrenbergianum Naeg.
Pediastrum sp.
Scenedesmus sp.
Coelastrum microporum Naeg.
Binuclearia tatrana Wittr.
Oedogonium sp.
Zygnema sp.
Spirogyra sp.
Sirogonium sp.
Gonatozygon Brebissonii De Bary
Genicularia spirotaenia De Bary
Netrium digitus (Ehrenb.) Itzigs. & Rothe
Closterium acerosum (Schrank) Ehrenb.
 var. angolense W. & G. S. West
C. setaceum Ehrenb.
C. cornu Ehrenb.
C. aciculare T. West. var subpronum W. & G. S. West
Cosmarium capitulum Roy & Biss.
C. depressum (Naeg.) Lund
C. rectangulare Grun.
C. pseudoarctoum Nordst.
Arthrodesmus phimus Turn.
Staurastrum clepsydra Nordst.
S. connatum (Lund) Roy & Biss.
S. Dickiei Ralfs
S. orbiculare Ralfs
S. Sebaldii Reinsch.
S. tumidum Bréb.
S. anatinum Cooke & Wills var. Lagerheimii (Schmidle) W. & G. S. West
S. sexangulare (Bulnh.) Lund
Stauroneis phoenicenteron Ehrenb.
Navicula radiosa Kütz.
Rhopalodia gibba (Ehrenb.) O. Müll.
Fragilaria crotonensis Kitton
F. construens (Ehrenb.) Grun. var. venter (Ehrenb.) Grun.
F. brevistriata Grun.
F. virescens Ralfs
Achnanthes minutissima Kütz. var. cryptocephala Grun.
Hantzschia amphioxys (Ehrenb.) Grun.
Frustulia rhomboides (Ehrenb.) de Toni
Dinobryon sertularia Ehrenb.
*Peridinium cinctum (Müll.) Ehrenb.
*P. Elpatiewskyi (Ostenf.) Lemm.
Microcystis pulverea (Wood) Mig.
Chroococcus dispersus (Keissl.) Lemm.
C. limneticus Lemm.
Merismopedia sp.
Tolypothrix tenuis Kütz.
Trichodesmium lacustre Kleb.

* Summer forms.

Quantitative determinations

A Sedgwick-Rafter counting cell (20 × 50 mm. in area and etched in millimetre squares) was used in counting the phytoplankton. The sample was thoroughly mixed by inverting the bottle 20 times. A quantity of the suspension equal to the volume of the cell (1·3 c.c.) was, with a pipette, transferred to it. The quantity of algae in this volume was estimated by counting the number of individuals in every third square (100 in all), and this was repeated 6 times for every sample; the average of the 6 counts being taken as the final figure. The total number of individuals in the known volume of lake water

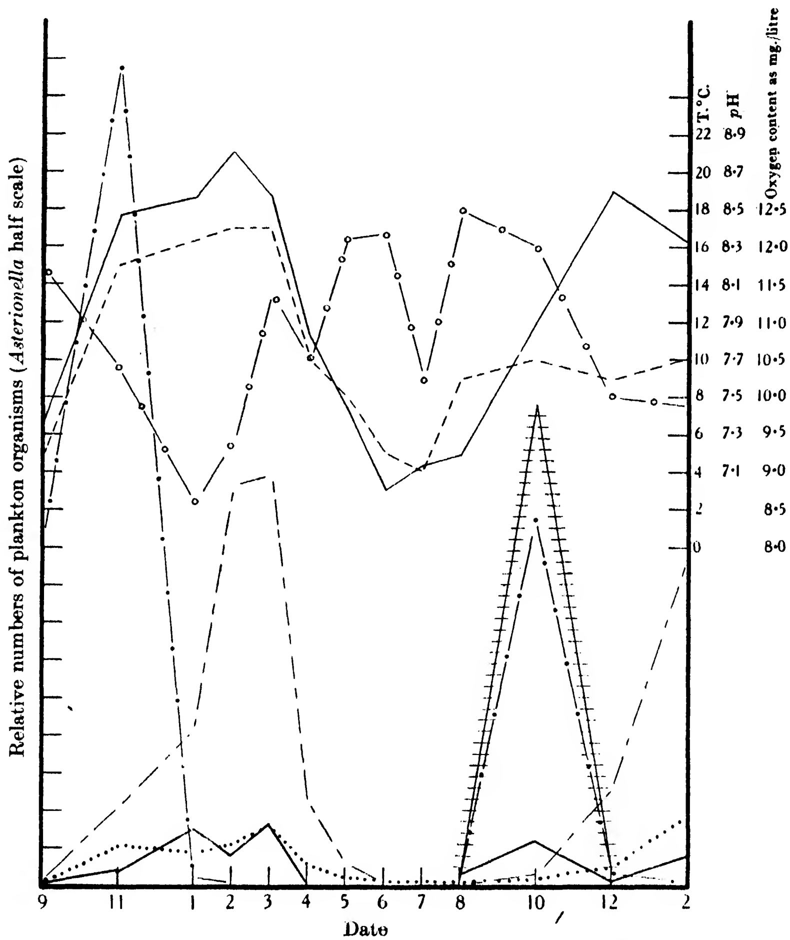

Fig. 1. Graphs showing (above) the range in temperature *p*H and oxygen content, and (below) the range of five representatives of the phytoplankton. Key. - - - = *p*H. —— = *T*° C. ○—○ = oxygen content. •—• = *Asterionella*. — — — = *Botryococcus*. -|-|-|- = *Dinobryon*. —— = *Pandorina*. ...... = *Aphanocapsa*.

(cf. p. 353) from which the plankton had been collected was determined from this figure by simple proportion. Ten species representative of the algal groups occurring in the plankton were chosen for these quantitative determinations, viz. *Pandorina morum*, *Eudorina elegans*, *Volvox aureus*, *Kirchneriella lunaris*, *Staurastrum Manfeldtii*, *Botryococcus Braunii*, *Asterionella gracillima*, *Epithemia sorex*, *Dinobryon sertularia* and *Aphanocapsa elachista*. Since *Asterionella gracillima* was usually found as a colony of four cells, the figure representing the total number of *Asterionella* cells in a square of the Sedgwick-Rafter frame was divided by 4 to give the number of *Asterionella* colonies.

The periodicity of the ten species estimated, as well as the variations in the temperature, *p*H and oxygen content, correspond approximately with the seasons of the year as shown in Fig. 1 (see also Table I).

Table I. *Showing the number of individuals, in thousands, in* 103 *l. of lake water*

The important maximum numbers are indicated in heavy type

Time	*Pandorina*	*Eudorina*	*Volvox*	*Kirchneriella*	*Staurastrum Manfeldtii*	*Botryococcus*	*Asterionella*	*Epithemia*	*Dinobryon*	*Aphanocapsa*
Sept.	1·10	0·10	—	—	—	0·9	**114·50**	0·2	**45·70**	0·2
Nov.	2·30	3·10	—	0·40	0·03	**12·3**	**261·30**	2·9	—	6·2
Jan.	9·30	4·70	0·07	0·30	0·07	**24·9**	2·70	4·6	—	5·2
Feb.	5·10	2·70	0·40	3·20	0·10	**64·1**	1·90	5·9	—	7·0
Mar.	**10·00**	2·70	1·30	**18·40**	0·80	**65·4**	—	0·9	—	**10·0**
Apr.	0·80	0·80	2·10	**12·00**	0·20	**13·7**	0·02	0·3	—	3·5
May	0·07	0·10	0·10	0·03	0·03	**3·6**	0·05	1·6	—	1·2
June	0·20	0·03	**1·40**	—	—	0·9	0·20	1·2	—	0·9
July	0·30	0·07	0·30	—	—	0·4	—	**1·9**	—	0·3
Aug.	1·80	0·07	0·07	—	0·03	0·2	0·60	1·7	0·03	0·8
Oct.	**7·50**	0·20	—	—	—	1·8	**117·10**	1·4	**77·00**	1·2
Dec.	0·70	2·00	0·10	0·40	0·10	**15·2**	3·60	6·5	2·50	3·4
Feb.	4·80	0·80	1·80	**136·10**	0·20	**50·7**	1·50	1·1	—	**11·0**

Spring (September to November). *Asterionella gracillima* (graphed on a more reduced scale than the other species) and *Dinobryon sertularia*, dominant and subdominant respectively, show a definite spring growth and at the end of the spring *Dinobryon* rapidly disappears. *Pandorina*, *Botryococcus* and *Aphanocapsa* increase and *Kirchneriella* and *Staurastrum Manfeldtii* appear in the plankton during the latter part of this season. Temperature and *p*H gradually rise and the oxygen content falls.

Summer (December to February). *Botryococcus* is the dominant alga except in February 1936, when *Kirchneriella* was the more abundant. *Pandorina* and *Aphanocapsa* continue to increase, while *Epithemia* and *Eudorina* are more frequent during these summer months, *Asterionella* falls off rapidly while *Volvox* appears in the plankton. The lake water is characterized by a high temperature and *p*H and a low oxygen content.

Autumn (March to May). *Botryococcus* still remains the dominant species and reaches a maximum in March. *Kirchneriella* and *Aphanocapsa* are subdominants. The latter as well as *Pandorina*, *Volvox* and *Staurastrum Manfeldtii* are most abundant in the autumn, although *Pandorina* and *Aphanocapsa* may often be already common in the late summer. *Epithemia* decreases in numbers. There is a fall in temperature and *p*H and a rise in oxygen content.

Winter (June to August). There is a marked reduction in the number of algae. *Volvox*, *Pandorina* and *Epithemia* are the most important, while *Botryococcus* and *Aphanocapsa* are less frequent. Towards the end of the winter *Asterionella* and *Dinobryon* reappear. There is a low temperature and *p*H and a high oxygen content.

In the English lakes (Pearsall, 1932) *Dinobryon divergens* has been found to follow a diatom maximum, and the conditions which favour this *Dinobryon* maximum are low silica content (below 0·05 part per 100,000) and a high N/P ratio. In Lake Sarah an abundance of *Dinobryon sertularia* occurred prior to, or coincided with, the diatom maximum, and was characterized by a high silica content (0·135 part per 100,000) and a low N/P ratio. The factors which are believed to influence the multiplication of *D. divergens* in English lakes do not therefore obtain in the case of *D. sertularia* in Lake Sarah.

The increase of the phytoplankton in spring coincides with the rise in temperature and *p*H and is accompanied by a fall in oxygen content; the summer maxima follow the highest *p*H and temperature. The same sequence occurs in the English lakes.

The fall in silica content between July and September may be correlated with the growth of *Asterionella gracillima*. The fact that this maximum occurs when phosphates are high and the N/P ratio is low lends support to the conclusion of Pearsall (1932), that the growth of *A. gracillima* in Ullswater is favoured by these conditions.

The fact that *Aphanocapsa* is most abundant at the end of the summer when a high organic content of the water is to be suspected, is in accordance with the occurrence of Blue Green algae in the plankton of other waters.

The writer is indebted to Prof. E. Percival who suggested this study and gave advice and criticism; to Mr C. E. Foweraker, and to Prof. F. E. Fritsch.

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FIFTH REPORT OF THE TRANSPLANT EXPERIMENTS OF THE BRITISH ECOLOGICAL SOCIETY AT POTTERNE, WILTSHIRE

By ERIC M. MARSDEN-JONES and W. B. TURRILL

Since the preparation of the fourth report (December 1935) the committee has met at University College, London, and at Potterne. General approval was expressed of the management of the experiments for 1936–7.

Clones of *Ononis* and of *Solanum dulcamara* var. *marinum* are ready for use when space on the plots is available. The redistribution of ramets of *Fragaria vesca* has been accomplished and the variations recorded for the past two years are given in this report. The new stocks of *Plantago major* (large variety) and of *Silene maritima* (narrow-leaved variety) have been in position on all soils for the two years 1936–7.

Soil temperature

This has been read, at approximately weekly intervals, for the two years, for all five soils, from ordinary chemical mercury thermometers with the bulb immersed in the soil to a depth of 13 cm. The results indicate great variation and irregularity. The soils at 13 cm. depth evidently gain and lose heat with considerable rapidity. On the whole, the chalky clay showed the lowest temperatures throughout the year, with relatively few exceptions and these mostly in the colder parts of the year. The detailed readings are available for examination to any interested member of the B.E.S.

The following table is given on request but it is doubtful if deductions should be drawn from these figures because of the large and irregular fluctuations from reading to reading which are masked or cannot be satisfactorily expressed by statistical treatment:

	Sand		Calcareous sand		Clay		Chalky clay		Potterne soil	
	1936	1937	1936	1937	1936	1937	1936	1937	1936	1937
Max.	26·50	28·00	25·50	27·50	24·50	24·50	21·50	24·00	25·50	26·50
Min.	3·00	1·25	3·00	1·50	2·75	1·50	2·50	1·25	2·50	1·50
Mean	11·97	13·24	11·71	13·09	11·24	12·28	10·40	11·85	11·66	12·61

Meteorological data

The total annual rainfall for 1936 was 712·5 mm. (28·5 in.) and for 1937 was 828·0 mm. (33·12 in.). There were 175 "rain days" in 1936 and 161 in 1937. In 1936 there were relatively dry periods in May and August. July and January were the wettest months. In 1937 there were relatively dry spells in November and at midsummer. February and January were the wettest months. In neither 1936 nor 1937 was there a prolonged period of marked drought.

METEOROLOGICAL DATA FOR 1936–7

		Temperature				Relative humidity		Rainfall			
		Max.		Min.				Rainfall in mm.		No. of "rain days"	
1936		° C.	° F.	° C.	° F.	Max.	Min.	Week	Month	Week	Month
Jan.	1–7	9·4	49	– 1·1	30	86	55	14·00		3	
	8–14	12·8	55	– 3·3	26	89	47	16·75		3	
	15–21	8·3	47	– 4·4	24	89	38	19·00		4	
	22–28	10·6	51	– 1·1	30	89	46	34·50		7	
	29–31	11·7	53	2·2	36	87	55	14·25	98·50	2	19
Feb.	1–7	10·6	51	– 6·7	20	86	25	4·00		2	
	8–14	6·7	44	– 5·0	23	89	28	3·50		1	
	15–21	10·6	51	– 4·4	24	88	29	37·00		6	
	22–28	9·4	49	– 3·9	25	88	29	5·25		4	
	29	4·4	40	– 0·6	31	85	70	3·50	53·25	1	14
Mar.	1–7	10·0	50	– 5·6	22	88	30	7·25		5	
	8–14	14·4	58	– 0·6	31	87	36	10·75		2	
	15–21	15·0	59	– 1·1	30	88	19	3·75		2	
	22–28	16·7	62	3·3	38	89	29	24·50		7	
	29–31	18·3	65	6·7	44	86	37	9·50	55·75	2	18
Apr.	1–7	10·0	50	– 2·2	28	87	36	15·50		2	
	8–14	12·2	54	– 3·3	26	88	30	2·50		3	
	15–21	14·4	58	– 3·3	26	87	12	25·25		5	
	22–28	18·3	65	– 5·0	23	87	17	6·25		3	
	29–30	17·2	63	0·0	32	89	24	0·00	49·50	0	13
May	1–7	22·8	73	1·7	35	88	22	2·25		1	
	8–14	26·1	79	4·4	40	86	10	10·75		1	
	15–21	29·4	85	2·2	36	86	17	1·50		3	
	22–28	25·6	78	– 0·6	31	90	12	1·75		2	
	29–31	18·9	66	1·1	34	89	19	0·75	17·00	2	9
June	1–7	19·4	67	1·7	35	87	28	17·00		4	
	8–14	23·3	74	6·1	43	86	25	15·75		5	
	15–21	33·3	92	5·6	42	86	30	27·50		3	
	22–28	30·6	87	10·0	50	86	14	12·50		1	
	29–30	24·4	76	12·8	55	85	38	23·00	95·75	1	14
July	1–7	25·6	78	10·6	51	85	32	21·00		5	
	8–14	20·6	69	7·2	45	85	33	45·25		7	
	15–21	24·4	76	6·7	44	84	32	12·50		4	
	22–28	22·8	73	5·6	42	84	19	24·25		5	
	29–31	22·2	72	6·7	44	85	26	5·75	108·75	2	23
Aug.	1–7	22·2	72	6·1	43	84	29	7·75		5	
	8–14	26·7	80	6·7	44	84	16	0·00		0	
	15–21	28·3	83	6·1	43	84	18	3·75		1	
	22–28	30·0	86	7·2	45	84	18	0·00		0	
	29–31	32·2	90	11·1	52	83	10	0·00	11·50	0	6
Sept.	1–7	28·9	84	11·1	52	83	25	15·25		3	
	8–14	21·7	71	6·7	44	83	41	19·75		4	
	15–21	23·9	75	8·3	47	82	30	14·25		4	
	22–28	21·7	71	– 0·6	31	84	32	6·75		3	
	29–30	13·3	56	0·0	32	82	29	0·00	56·00	0	14
Oct.	1–7	20·0	68	– 2·8	27	83	19	0·00		0	
	8–14	17·2	63	0·0	32	82	28	2·25		2	
	15–21	17·8	64	1·7	35	82	30	1·75		2	
	22–28	15·0	59	– 1·1	30	80	29	19·50		5	
	29–31	15·6	60	– 1·1	30	81	58	18·25	41·75	3	12

		Temperature				Relative humidity		Rainfall			
		Max.		Min.				Rainfall in mm.		No. of "rain days"	
1936		° C.	° F.	° C.	° F.	Max.	Min.	Week	Month	Week	Month
Nov.	1–7	11·1	52	1·7	35	81	44	39·50		6	
	8–14	14·4	58	– 1·1	30	83	40	25·00		6	
	15–21	13·3	56	– 3·9	25	81	41	6·25		2	
	22–28	6·7	44	– 3·9	25	79	58	1·00		1	
	29–30	11·1	52	4·4	40	72	44	3·50	75·25	1	16
Dec.	1–7	11·7	53	– 6·7	20	80	27	6·50		4	
	8–14	10·6	51	– 4·4	24	78	55	19·00		5	
	15–21	12·8	55	2·2	36	79	42	11·00		4	
	22–28	10·0	50	– 2·2	28	78	48	5·50		2	
	29–31	10·0	50	0·0	32	76	19	7·50	49·50	2	17
1937											
Jan.	1–7	9·4	49	– 2·2	28	78	38	10·00		5	
	8–14	10·0	50	– 2·2	28	76	48	10·50		2	
	15–21	10·6	51	– 2·2	28	78	41	48·25		7	
	22–28	9·4	49	– 3·3	26	77	48	26·75		5	
	29–31	8·9	48	– 2·8	27	76	61	17·00	112·50	3	22
Feb.	1–7	10·0	50	– 1·1	30	76	21	53·00		5	
	8–14	11·1	52	– 3·3	26	78	28	6·25		6	
	15–21	10·0	50	0·0	32	74	25	22·75		6	
	22–28	10·0	50	– 2·2	28	73	20	44·00	126·00	7	24
Mar.	1–7	7·8	46	– 3·3	26	71	27	8·75		2	
	8–14	10·0	50	– 5·6	22	87	25	48·25		5	
	15–21	12·2	54	– 2·8	27	76	21	24·00		7	
	22–28	10·0	50	– 5·6	22	74	17	3·50		2	
	29–31	13·3	56	– 4·4	24	72	17	0·00	84·50	0	16
Apr.	1–7	16·7	62	0·6	33	71	17	18·00		4	
	8–14	15·6	60	2·2	36	70	18	25·75		4	
	15–21	14·4	58	1·7	35	66	19	13·75		5	
	22–28	17·8	64	– 1·1	30	71	10	3·75		1	
	29–30	17·8	64	0·6	33	66	22	0·00	61·25	0	14
May	1–7	23·9	75	0·0	32	70	13	2·50		1	
	8–14	20·0	68	3·3	38	70	12	14·75		5	
	15–21	22·2	72	1·7	35	59	12	4·25		1	
	22–28	26·1	79	5·6	42	66	10	26·25		3	
	29–31	28·3	83	3·3	38	95	11	0·00	47·75	0	10
June	1–7	25·6	78	4·4	40	95	25	0·00		0	
	8–14	30·6	87	6·7	44	95	23	21·50		4	
	15–21	22·8	73	3·9	39	95	16	8·50		3	
	22–28	25·0	77	6·7	44	95	16	1·50		2	
	29–30	19·4	67	3·3	38	95	27	0·25	31·75	1	10
July	1–7	28·9	84	4·4	40	95	24	9·50		2	
	8–14	27·8	82	8·9	48	95	35	5·50		4	
	15–21	30·6	87	5·0	41	95	29	20·00		4	
	22–28	22·2	72	6·7	44	90	32	1·75		1	
	29–31	27·2	81	7·8	46	95	23	0·00	36·75	0	11
Aug.	1–7	32·8	91	8·9	48	90	11	0·00		0	
	8–14	31·1	88	6·7	44	90	17	38·25		5	
	15–21	22·8	73	6·7	44	91	31	5·00		2	
	22–28	27·8	82	6·7	44	95	24	0·00		0	
	29–31	27·8	82	8·3	47	92	28	1·75	45·00	1	8

1937		Temperature Max. °C.	Temperature Max. °F.	Temperature Min. °C.	Temperature Min. °F.	Relative humidity Max.	Relative humidity Min.	Rainfall in mm. Week	Rainfall in mm. Month	No. of "rain days" Week	No. of "rain days" Month
Sept.	1–7	25·0	77	7·2	45	95	28	3·75		2	
	8–14	23·3	74	1·1	34	95	16	10·75		4	
	15–21	17·8	64	2·2	36	93	43	87·00		5	
	22–28	22·2	72	5·6	42	95	28	1·25		1	
	29–30	20·0	68	7·8	46	95	30	0·00	102·75	0	12
Oct.	1–7	22·2	72	1·7	35	95	32	0·75		2	
	8–14	15·6	60	1·1	34	95	25	0·00		0	
	15–21	17·8	64	0·6	33	95	31	2·75		1	
	22–28	13·9	57	4·4	40	94	39	84·75		7	
	29–31	12·8	55	5·6	42	91	64	11·75	100·00	3	13
Nov.	1–7	18·3	65	0·6	33	93	54	3·50		1	
	8–14	10·0	50	−7·8	18	95	32	2·50		1	
	15–21	6·7	44	−9·4	15	95	51	6·25		2	
	22–28	10·0	50	−6·7	20	93	70	11·00		1	
	29–30	10·0	50	4·4	40	92	60	8·75	32·00	2	7
Dec.	1–7	8·9	48	−6·1	21	93	44	24·50		4	
	8–14	6·1	43	−8·3	17	94	55	13·50		4	
	15–21	8·9	48	−6·7	20	94	47	7·50		3	
	22–28	7·8	46	−1·1	30	92	58	2·00		3	
	29–31	2·8	37	−4·4	24	94	61	0·25	47·75	1	15

Biotic factors

Moss growth and slug attack were both, on the whole, greater than in 1934 and 1935, but frosts checked slug activity in December 1937. *Cladonia* sp. with podetia is still limited to the sand, on which it occurs in isolated clumps and in large patches up to a foot square, especially associated with the plants of both species of *Phleum*, and increased in size from 1936 to 1937.

Worm action continued to be marked on chalky clay and calcareous sand, but was less in 1937 than in 1936. A little was also observed on the other soils, least on clay. A single heap of material on the former weighed 11 oz. and on the latter 4½ oz. Still attached young shoots of freshly transplanted *Silene maritima* on clay and Potterne soils were pulled by worms into their holes.

Small grasshoppers were noticed on Potterne soil among *Phleum nodosum* in 1936: by July 1937 they had spread to all soils but were still limited to *P. nodosum* and remained most frequent on Potterne soil.

A single specimen of long-tailed field mouse (*Apodemus sylvaticus*) made a long tunnel in calcareous sand and threw up much material. It was captured in November 1937.

Moles have made several runs through the *Centaurea* plot on Potterne soil.

On the whole the Bryophyta were most abundant on calcareous sand, on the plots with least dense smother of plant growth throughout the year, and on the least disturbed surfaces. The general sequence, most first, for both years, was: calcareous sand, Potterne soil, sand, chalky clay, clay.

On 23. xii. 37, the following species of mosses were collected:

Sand. *Pottia truncatula* Lindb., *Ceratodon purpureus* Brid., *Brachythecium rutabulum* B. & S., *Dicranella heteromalla* Schp., *Eurhynchium confertum* Milde.

Calcareous sand. *Barbula unguiculata* Hedw. (much), *B. convoluta* Hedw., *Brachythecium rutabulum* B. & S. (only on and near *Centaurea* plot).

Clay. *Barbula unguiculata* Hedw., *Fissidens taxifolius* Hedw., *Ceratodon purpureus* Brid.

Chalky clay. *Barbula unguiculata* Hedw., *Fissidens taxifolius* Hedw., *Pottia* sp. (very little).

Potterne soil. *Brachythecium rutabulum* B. & S. (on *Centaurea* plot only and very little), *Pottia truncatula* Lindb., *Dicranella heteromalla* Schp., *Ceratodon purpureus* Brid., *Barbula unguiculata* Hedw.

Small patches of *Vaucheria* sp. mixed with filaments of *Hormidium* sp. were present on the clay and chalky clay in December 1937.

Centaurea nemoralis Jord. forma **radiata albiflora**

Seasonal condition and deaths. This plant has maintained its growth fairly well on all soils. The only additional deaths to record are Nos. 69 and 72 on clay and No. 149 on Potterne soil. Nos. 69 and 149 died in the spring of 1936 and No. 72 in the autumn of 1937. The spring growth was recorded on 1. iii. 36 and 9. iii. 37 and (most first) in the sequence: sand, calcareous sand, chalky clay, clay, Potterne soil. The winter growth, recorded on 23. xii. 37, was (most first): chalky clay, clay, sand, calcareous sand, Potterne soil.

Seedlings.

	1. iii. 36	18. iv. 36	30. v. 36	8. vii. 36	4. x. 36	24. xii. 36
Sand	None	Very numerous	Very numerous	None	Few	Very few
Calcareous sand	None	Very numerous	Numerous	None	Numerous	Very few
Clay	None	Numerous	Few	None	Very few	Very few
Chalky clay	None	Few	Numerous	None	Very few	Very few
Potterne soil	None	Numerous	Numerous	None	Very few	None

	7. iii. 37	18. v. 37	23. vii. 37	17. x. 37	23. xii. 37
Sand	Few	Numerous	None	Very numerous	Few
Calcareous sand	Few	Very numerous	Numerous	Numerous	Few
Clay	Very few	Few	Few	Few	None
Chalky clay	Very few	Few	Very few	Very numerous	Few
Potterne soil	Very few	Very few	None	Very few	None

The best germination was in spring and autumn and again on the sands.

General tone. The sequence (best first) has, on the whole, been maintained as follows: sand, calcareous sand, chalky clay, clay, Potterne soil.

Habit. The marked difference in habit between the plants at Kew (widely ascending stems) and those on all the soils at Potterne (erect stems) was maintained.

The natural cloning on all soils is still increasing. The amount of cloning, on 23. xii. 37 in the sequence, was: sand (most), clay, calcareous sand, chalky clay, Potterne soil (least).

Numbers of flowering stems per ramet.

	Sand		Calcareous sand		Clay		Chalky Clay		Potterne soil	
	1936	1937	1936	1937	1936	1937	1936	1937	1936	1937
Total ramets	26	26	26	26	19	19	20	20	23	23
Total stems per soil	1549	2243	1299	1621	562	1100	1005	1347	716	927
Max. per ramet	95	152	112	150	65	89	81	112	96	100
Min. per ramet	16	21	8	7	7	24	5	11	7	7
Mean per ramet	59·6	86·3	50·0	62·3	29·6	57·9	50·2	67·3	31·1	43·0
Standard deviation	21·5	32·3	30·0	40·0	17·3	17·7	21·6	29·0	20·2	21·1

First flowering.

	1936					1937				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
18 June	—	—	—	—	—	1	1	—	—	—
19	—	1	1	—	—	2	1	1	—	—
20	—	2	2	1	—	3	7	2	—	—
21	3	3	4	1	—	3	14	6	2	2
22	5	7	10	5	3	4	18	10	5	3
23	8	15	12	12	7	9	26	13	11	9
24	10	19	15	15	13	19	—	15	15	15
25	18	23	16	18	18	26	—	19	18	19
26	24	25	18	19	20	—	—	—	20	21
27	25	26	18	19	23	—	—	—	—	22
28	26	—	18	19	—	—	—	—	—	23
29	—	—	19	20	—	—	—	—	—	—

Primary flowering. Maximum flowering on all soils was scored for 6. vii. 36 and 1. vii. 37.

Completion of primary flowering. The sequence (the first completed placed first) was: (20. vii. 36) calcareous sand, Potterne soil, sand, chalky clay, clay; (17. vii. 37) calcareous sand, sand, clay, chalky clay, Potterne soil.

Secondary flowering. On 1. viii. 36 the descending sequence was: clay, chalky clay, sand, Potterne soil, calcareous sand.

Fungus on dead stems. Fructifications of the saprophyte *Hypholoma sublateritium* appeared in October 1936 on the dead lower parts of three *Centaurea* ramets on the sand and one on calcareous sand; in November 1937 on three ramets on the calcareous sand.

Silene maritima L.

Origin of immediate parent (S.P. 68). Chesil Beach, Portland end, March 1932.

Description. Habit, semi-prostrate, spreading, stems very slender up to 3·2 dm. long, with abundant anthocyanin in vegetative parts; with barren stems. *Leaves* very uniform, except for fluctuations in size at different nodes, linear or narrowly lanceolate- or oblanceolate-linear, acute, slightly apiculate, slightly narrowed to the base, uppermost pair on flowering stems slightly amplexicaul, up to 2·2 cm. long, 4 mm. broad, very few widely scattered short cilia, somewhat fleshy, very dark glaucous green suffused with dark antho-

cyanin. *Inflorescence* of 1–3 flowers, erect when in bloom. *Bracts* glabrous, not ciliate, lower green, herbaceous, similar to the uppermost leaves, upper smaller and narrower and becoming completely scarious. *Calyx* narrow-cylindric in flower, 1·7 cm. long, 0·6–0·8 cm. diam., in fruit obovoid-cylindric, deeply coloured with anthocyanin. *Corolla* with petals divided three-quarters length of lamina, some petals multilobed; segments and petals not overlapping, 2·1 cm. long, 0·9–1·0 cm. broad; corona of well-developed scales; diam. of corolla 1·9–2·4 cm. Most flowers female, occasional hermaphrodite flowers with from 1 to 10 stamens with coloured anthers and filaments. *Stigmata* coloured. *Immature seeds* coloured. *Ripe capsules* obloid, without the teeth 5 mm. long, 5 mm. broad (in broadest part). Teeth each an isosceles triangle 2 mm. long, 1·5 mm. broad at base, strongly recurved. *Carpophore* 3·5 mm. long, 2 mm. broad. *Mature seeds* in flat outline broadly hemispherical, 2 mm. long, 1·5 mm. broad, armadillo.

In *Kew Bulletin*, 1929, p. 171, we described a peculiar population of *S. maritima* which occurs as an isolated group at the Portland end of the Chesil Beach, Dorset. The plants of this population are especially characterized by slender habit, narrow leaves, and usually much anthocyanin. Certain individuals from this population have been much used in genetical research, of which some has already been published (see series of papers in *Kew Bulletin*, 1928–37). A plant collected on 27. iii. 32 was grown at Potterne in the experimental grounds. This plant was selfed (N. 105) in 1933 and 91 offspring raised. The selfed family was uniform and like the parent for habit and foliage characters and for deep anthocyanin of the vegetative parts. Plant No. 6 of N. 105 was cloned at Kew in the summer of 1935 and the ramets planted into the transplant beds at Potterne on 18. iv. 36. On 25. iv. 36 the tone of the ramets on all soils was good.

Deaths. No deaths occurred in 1936 or in the winter 1936–7. The following plants died between 9. iii. 37 and 10. v. 37. Nos. 2, 4, 5, 9, 19, all on the sand. Between 10. v. 37 and 17. x. 37 the following additional deaths, all on the sand, were recorded: Nos. 1, 3, 7, 8, 12, 14, 15, 16. No deaths have occurred on the other soils.

Habit and foliage. There has been so far no change in general habit or gross morphological characters on any of the soils. The ramets all retain the slender habit, narrow leaves, narrow-cylindric calyx, and very much anthocyanin of N. 105/6. There was a slight indication when the ramets were viewed in mass that the leaves were a little smaller on the sands, intermediate on the clays, and largest on the Potterne soil. This refers to gross size not to any change of shape. It was impossible to express these apparent slight differences by valid statistics.

The 1936–7 winter was comparatively mild. As a result a proportion of the previous year's green "barren" shoots were retained (die-back chamaephyte) on all soils over the winter. Dying-back was recorded (9. iii. 37) in the following

sequence (least first) chalky clay, calcareous sand, sand, clay, Potterne soil. New growth arises in early spring from the centre of the ramets, on all soils, forming a nearly erect tuft of flowering stems. Flower buds were first recorded on some plants on sand, clay, and chalky clay on 9. iii. 37. Last year's stems form a circle adpressed to the soil outside the new growth. On some of these old stems on sand and clay last year's capsules were still retained. In December 1937, frosts caused considerable browning on all soils.

General tone (best first).

30. v. 36	6. vii. 36	22. ix. 36	24. xii. 36
Potterne soil	Potterne soil	Potterne soil	Potterne soil
Sand	Sand	Clay	Clay
Clay	Clay	Sand	Chalky clay
Calcareous sand	Calcareous sand	Chalky clay	Sand
Chalky clay	Chalky clay	Calcareous sand	Calcareous sand

9. iii. 37	10. v. 37	6. vii. 37	17. x. 37	23. xii. 37
Potterne soil	Chalky clay	Potterne soil	Potterne soil	Potterne soil
Clay	Clay	Chalky clay	Chalky clay	Chalky clay
Chalky clay	Potterne soil	Clay	Clay	Clay
Sand	Sand	Sand	Calcareous sand	Calcareous sand
Calcareous sand	Calcareous sand	Calcareous sand	Sand	Sand

Ramet diameters in cm. (taken 2. vii. 37).

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	21	26	26	26	26
Maximum diameter	55	54	63	70	70
Minimum diameter	43	22	49	41	38
Mean diameter	50·1	41·5	55·7	58·9	63·1
Standard deviation	3·5	7·8	4·1	7·0	6·7

First flowering.

In 1936 the ramets had not all become fully established before flowering commenced. As a result, first flowering was very irregular, extending from 26. v. 36 to 9. ix. 36. The following numbers of ramets did not flower at all: 11 on calcareous sand, 6 on clay, and 9 on chalky clay.

Maximum floricfery occurred on 27. v. 37 on all soils. Primary flowering was nearing completion on 6. vii. 37 and was scored in the following sequence (most nearly completed first): calcareous sand, sand, clay, chalky clay, Potterne soil.

N. 105/6 was a plant producing large numbers of female flowers, but with very few hermaphrodite flowers. The transplant ramets also produced mainly female flowers. The seasonally earlier flowers were, with very few exceptions, female, but most ramets later in the season had some (in varying proportions) hermaphrodite flowers. On 16. v. 37 all the flowers then at anthesis were female. On 9. vii. 37 hermaphrodite flowers occurred on all plants except 1 on sand, 3 on calcareous sand, 1 on clay, and 1 on chalky clay. On the gynomonoecious plants the number of female flowers ranged on sand from 1 to 34, on calcareous sand from 1 to 5, on clay from 1 to 12, on chalky clay from 1 to 18, and on Potterne soil from 1 to 51.

The following table gives the first flowering for 1937:

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
30 April	—	1	2	—	—
1 May	—	1	2	—	—
2	5	1	4	8	—
3	7	3	6	23	—
4	16	3	10	24	—
5	18	3	14	24	—
6	18	5	16	24	1
7	21	9	20	25	2
8	—	14	24	25	3
9	—	14	24	25	3
10	—	16	24	26	5
11	—	16	25	—	7
12	—	16	25	—	10
13	—	16	25	—	10
14	—	18	26	—	14
15	—	18	—	—	14
16	—	18	—	—	14
17	—	18	—	—	16
18	—	18	—	—	17
19	—	18	—	—	18
20	—	19	—	—	18
21	—	19	—	—	19
22	—	19	—	—	20
23	—	20	—	—	21
24	—	20	—	—	21
25	—	20	—	—	22
26	—	20	—	—	22
27	—	20	—	—	22
28	—	20	—	—	22
29	—	22	—	—	22
30	—	22	—	—	22
31	—	22	—	—	22
1 June	—	22	—	—	24
2	—	24	—	—	24
3	—	—	—	—	24
4	—	—	—	—	24
5	—	—	—	—	25
6	—	—	—	—	26

Seed set very badly, probably because of the large proportion of female flowers; most was set on Potterne soil.

Seedlings.

	4. x. 36	24. xii. 36	9. iii. 37	18. v. 37	23. vii. 37	17. x. 37	23. xii. 37
Sand	None	Few	Few	Very few	Few	Numerous	Few
Calcareous sand	None	None	None	Very few	None	Very few	None
Clay	None	None	None	Very few	Few	Very few	None
Chalky clay	None	None	None	Numerous	None	None	None
Potterne soil	None	None	Very few	None	None	None	None

Plantago major L.—*large variety*

Origin. Waylands, Potterne, Wilts., 27. iv. 1934.

Description (of plant before cloning). *Habit,* tall-growing robust plant, 9 dm. in diam., with a very large number of semi-strict leaves, 5·2 dm. above ground. *Leaves* with broadly elliptic ovate lamina with obtuse to rounded apex and cuneate base, in well-formed mature leaves 2·0–2·8 dm. long, 1·1–1·9 dm. broad, entire to coarsely crenate-undulate at the margins, with 7 to 9 conspicuous veins and 2 to 4 fainter lateral ones, shortly hispid on both surfaces;

petiole 1·6–2·6 dm. long. *Flowering spike* up to 6·6 dm. long, peduncle (up to first flowers) 3·5 dm. long, with short adpressed hairs in upper part, and fewer subspreading hairs in lower part; lowest bracts foliaceous, up to 4 cm. long and 3 cm. broad; flowers very numerous.

The plant as originally collected was a large plant with flat leaves. Within two months of transplanting to the Potterne Experimental Ground it showed signs of becoming semi-strict and within another month the plant was completely semi-strict. At this time (11. vii. 34) the diameter of the plant was 7·2 dm., the height of leaves above ground 2·5 dm., and the flowering spike 4 dm.

The original plant was cloned in the autumn of 1934 and 12 ramets were obtained. These were grown till October 1935 and remained uniformly large-leaved, semi-strict, and with foliaceous bracts. They were recloned at this date producing 75 ramets. These ramets were transplanted to the respective soils on 13. iv. 36. The ramets were not exactly uniform in crown size though every one had a single crown. The largest crowns were planted in the sands, those of intermediate size on the clays, and the smallest on Potterne soil. The differences were slight.

The original plant was selfed under control in 1934. A family of 43 plants flowered in 1935. These were uniform for the parental characters. One of these selfed plants was selfed under control and 50 offspring plants raised. These again were uniform and as the parent, except for slight fluctuations on the same plant and fluctuation from semi-strict to strict.

Deaths. No deaths occurred on any of the soils during 1936. In March 1937 ramet No. 31, on calcareous sand, and in May 1937 ramet No. 14, on sand, died.

General tone.

30. v. 36	6. vii. 36	24. xii. 36	10. v. 37	6. vii. 37	17. x. 37
Potterne soil	Potterne soil	Potterne soil	Potterne soil	Potterne soil	Potterne soil
Calcareous sand	Clay	Clay	Chalky clay	Chalky clay	Chalky clay
Sand	Chalky clay	Chalky clay	Clay	Clay	Clay
Chalky clay	Calcareous sand	Calcareous sand	Calcareous sand	Sand	Sand
Clay	Clay	Sand	Sand	Calcareous sand	Calcareous sand

Mildew attacked the plants as follows: 22. ix. 36, on clay much, on Potterne soil little, on other soils none; 17. x. 37, on sand little, on calcareous sand little, on clay much, on chalky clay little, on Potterne soil much. No attack of *Ramularia plantagineae* has so far occurred.

Anthocyanin coloration.

	6. vii. 36	23. ix. 36
Sand	Very much	Little
Calcareous sand	Much	Very much
Clay	Little	Very much
Chalky clay	Little	Much
Potterne soil	Very little	Much

Indumentum, 6. viii. 36. The extreme base of the older peduncles glabrous, lower parts with spreading hairs, upper parts with adpressed hairs. On the sand the indumentum was less dense. On 6. vii. 37 the indumentum was less and adpressed on chalky clay.

Foliaceous bracts were present on ramets on all soils. The degree of their development was correlated with the vigour of the spikes.

Seedlings.

	4. x. 36	24. xii. 36	18. v. 37	23. vii. 37	17. x. 37	23. xii. 37
Sand	Very few	None	Very numerous	Very numerous	Very few	None
Calcareous sand	Very few	None	Numerous	Very numerous	Numerous	Few
Clay	Few	None	Very few	Few	Very few	None
Chalky clay	Very few	None	Very numerous	Few	None	None
Potterne soil	Numerous	None	Very numerous	Few	None	None

Infructescences are retained with some seeds unshed from the capsules up to at least the end of July of the second year.

Commencement of winter-rest period. The sequence (earliest "dormant" first) was clay, calcareous sand, Potterne soil, chalky clay, sand, for 1936, and calcareous sand, sand, Potterne soil, clay, chalky clay, for 1937.

Size of winter rosette buds. The sequence (largest first) was Potterne soil, clay, chalky clay, calcareous sand, sand.

Commencement of spring growth (9. iii. 37). The sequence (earliest first) was Potterne soil, clay, chalky clay, sand, calcareous sand.

Retention of depth. None of the plants showed heaving up ("lifting") after frost or other weather changes on any of the soils.

Habit. Full records have been kept of the behaviour of individual ramets throughout the two years. The ramets at the last scoring before transplanting were semi-strict. Six weeks after transplanting all rosettes became flat, except five which were semi-strict. At the end of the 1936 growing season (22. ix. 36) the ramets were nearly all semi-strict except on the sand where two were semi-strict and the remainder more or less flat. During 1937, clay, chalky clay, and Potterne soil ramets were strict, those on the sands fluctuated between flat and semi-strict. On the whole the ramets are flatter on the sands where they are smaller and have fewer leaves and more or less strict on the clays and Potterne soil where they are larger and have more leaves.

Diameters of ramets, in cm.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
30. v. 36					
Max. diameter	34	37	41	29	43
Min. diameter	22	25	15	19	23
Mean diameter	26·6	30·3	30·6	24·3	34·2
6. viii. 36					
Max. diameter	61	63	91	74	91
Min. diameter	39	54	61	47	66
Mean diameter	49·9	58·6	75·9	66·1	78·3
22. vii. 37					
Max. diameter	60	52	98	98	116
Min. diameter	37	29	60	45	49
Mean diameter	49·5	44·8	74·1	82·4	82·3

Height of vegetative parts, in cm.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
22. vii. 37					
Max. height	23	15	46	53	66
Min. height	8	7	23	31	30
Mean height	13·7	11·8	35·4	43·9	41·4

Length and breadth of largest leaves per ramet, in cm.

1936	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	14	14	14	14	14
Max. length	18	21	28	25	30
Min. length	11	15	20	15	20
Mean length	14·40	17·90	24·40	21·10	25·30
Standard deviation	1·76	1·80	2·43	2·92	2·69
Max. breadth	13	15	20	18	18
Min. breadth	9	11	14	10	14
Mean breadth	10·40	12·60	16·60	15·30	16·30
Standard deviation	1·07	1·15	1·64	2·25	1·34
Correlation l. and b.	0·86	0·90	0·79	0·92	0·65
1937					
Number of ramets	13	13	14	14	14
Max. length	18	16	25	25	28
Min. length	11	10	17	14	18
Mean length	15·20	13·90	20·30	21·60	22·50
Standard deviation	1·83	1·71	2·00	2·53	2·85
Max. breadth	14	12	21	18	19
Min. breadth	9	6	13	11	13
Mean breadth	11·90	9·80	16·10	15·20	16·90
Standard deviation	1·55	1·52	2·27	1·86	1·77
Correlation l. and b.	0·68	0·86	0·88	0·89	0·87

Number of crowns (rosettes) per ramet, 9. iii. 37.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	14	13	14	14	14
Maximum	5	6	9	8	8
Minimum	1	1	2	1	3
Mean	1·4	4·6	6·0	5·1	5·1
Total per soil	20	60	84	71	72

Number of flowering spikes per ramet.

1936	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	14	14	14	14	14
Maximum	46	45	111	92	82
Minimum	13	15	24	16	23
Mean	19·9	29·1	64·4	54·6	57·2
Standard deviation	9·0	9·6	25·0	22·0	15·9
1937					
Number of ramets	13	13	14	14	14
Maximum	56	30	106	106	173
Minimum	12	5	43	31	39
Mean	32·8	20·1	63·9	72·4	77·1
Standard deviation	16·8	7·1	21·7	22·7	36·9

Height of flowering stems per ramet, in cm.

1936	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Number of ramets	14	14	14	14	14
Maximum	50	54	70	64	68
Minimum	25	31	47	39	47
Mean	37·7	45·2	58·6	53·4	57·2
Standard deviation	6·9	5·6	6·1	7·2	5·3
1937					
Number of ramets	13	13	14	14	14
Maximum	53	46	61	71	66
Minimum	33	28	45	48	40
Mean	43·8	39·3	52·9	60·4	51·4
Standard deviation	5·4	4·5	5·2	6·8	6·2

First flowering.

	1936					1937				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
27 June	—	—	1	—	1	—	—	—	—	—
28	—	—	1	—	2	2	—	—	—	—
29	—	—	1	—	3	2	—	—	—	—
30	—	1	1	—	3	2	—	—	—	—
1 July	—	1	1	—	4	2	1	—	—	—
2	—	2	2	—	4	3	1	—	1	—
3	1	7	2	1	5	3	1	—	1	—
4	2	8	4	2	6	6	2	—	1	1
5	3	8	4	2	6	7	2	—	2	1
6	5	9	4	4	6	9	2	—	5	1
7	5	9	4	4	6	11	3	—	7	1
8	5	10	6	8	7	12	4	—	7	1
9	6	10	6	8	7	12	5	—	9	1
10	6	10	6	9	8	12	5	—	9	2
11	6	10	7	9	9	12	6	—	9	3
12	8	11	7	9	12	12	9	1	11	4
13	10	13	7	9	13	12	11	3	13	6
14	10	13	10	11	14	13	12	5	13	6
15	11	13	11	11	—	—	13	9	13	7
16	12	13	12	11	—	—	—	10	14	11
17	12	14	12	14	—	—	—	12	—	12
18	13	—	12	—	—	—	—	12	—	13
19	—	—	12	—	—	—	—	13	—	13
20	—	—	12	—	—	—	—	13	—	13
21	—	—	12	—	—	—	—	14	—	14
26	—	—	12	—	—	—	—	—	—	—
27	—	—	14	—	—	—	—	—	—	—

Phleum pratense L.

Deaths. No further deaths have occurred on any of the soils.

General tone. The sequence throughout the two years has been in the following descending order: Potterne soil, clay, chalky clay, sand, calcareous sand. A tendency for death of central shoots in some ramets, especially on the clay, was noticed in 1937. This may indicate the commencement of "fairy-ring" growth. After heavy rain the tall flowering stems on Potterne soil show temporary lodging in the summer months. The ramets in the vegetative condition have more or less compact growth. The sequence, most compact first, has held for the two years as follows: calcareous sand, sand, chalky clay, clay, Potterne soil. Plants on Potterne soil have the deepest green colour, those on the clays are intermediate, and those on the sands yellowish green. *Hypholoma sublateritium* occurred as a saprophyte on decaying debris of ramet 32 on calcareous sand.

Surface roots. In March of both years masses of fibrous roots were visible at the surface of the soil on all beds, most on Potterne soil. They were mainly dirty brown in colour. On sand and Potterne soil large root mats were visible in December 1937, but few were present at the surface on the other soils.

Maximum heights of flowering stems per ramet, in cm.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
1936					
Number of ramets	26	26	25	25	26
Maximum	113	120	158	143	150
Minimum	90	90	113	113	135
Mean	101·4	100·6	135·2	126·3	143·4
Standard deviation	6·8	7·7	10·6	7·5	4·2
1937					
Number of ramets	26	26	25	25	26
Maximum	113	105	143	128	150
Minimum	90	75	98	105	128
Mean	99·7	88·2	128·3	120·5	136·7
Standard deviation	6·2	7·8	9·7	6·8	6·4

Number of flowering stems per ramet.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
1936					
Number of ramets	26	26	25	25	26
Maximum	75	42	125	106	176
Minimum	24	6	34	32	41
Mean	44·3	17·7	69·2	64·2	117·5
Standard deviation	13·1	9·1	26·0	25·8	42·4
Total per soil	1152	459	1729	1604	3055
1937					
Number of ramets	26	26	25	25	26
Maximum	64	25	98	89	167
Minimum	23	3	20	23	42
Mean	38·7	12·4	48·0	45·6	105·4
Standard deviation	13·0	5·5	19·8	19·8	34·8
Total per soil	1006	323	1200	1139	2741

Seedlings.

	1. iii. 36	8. vii. 36	4. x. 36	24. xii. 36
Sand	Numerous	Few	Very numerous	Very numerous
Calcareous sand	Very few	None	Very numerous	Very numerous
Clay	Very few	None	Very numerous	Few
Chalky clay	Very few	None	Very numerous	Few
Potterne soil	Numerous	Few	Very numerous	Very numerous

	18. v. 37	23. vii. 37	23. xii. 37
Sand	Numerous	Few	Numerous
Calcareous sand	Numerous	Very few	Numerous
Clay	Few	None	Numerous
Chalky clay	Few	Few	Numerous
Potterne soil	Very numerous	Few	Numerous

First flowering.

	1936					1937				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
29 June	6	—	1	5	1	—	—	—	—	—
30	6	—	1	5	1	—	—	—	—	—
1 July	21	8	1	19	1	1	—	—	—	—
2	26	19	21	25	2	26	26	25	25	14
3	—	23	21	—	2	—	—	—	—	22
4	—	25	22	—	3	—	—	—	—	26
5	—	26	25	—	26	—	—	—	—	—

Maximum florifery on all soils occurred on 6. vii. 36 and on 3. vii. 37, except for Potterne soil, which attained maximum on 8. vii. 37.

Phleum nodosum L.

Deaths. No deaths have occurred on any of the plots.

General tone. The sequence (best first) has been maintained as Potterne soil, clays, sands, with certain fluctuation between clay and chalky clay and sand and calcareous sand respectively.

The rounded hummock habit became even more marked; the order, most compact first, was calcareous sand, sand, chalky clay, clay, Potterne soil. On clay some dying of shoots in the centre of ramets was noted. New spring growth (early March) maintained the sequence (most first): Potterne soil, clay, chalky clay, sand, calcareous sand. The differences were very slight in 1937. Winter green was recorded, 23. xii. 37, most first, in the following sequence: Potterne soil, clay, chalky clay, sand, calcareous sand.

Surface roots. Brownish roots appeared just above the surface on sand, calcareous sand, and Potterne soil, but only in small numbers.

Seedlings. The clone remains self-sterile and no seedlings have appeared.

Maximum heights of flowering stems per ramet, in cm.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
1936					
Number of ramets	26	26	26	26	26
Flowering ramets	26	23	26	26	26
Maximum	51	36	71	71	76
Minimum	20	7	59	62	62
Mean	35·2	18·9	64·5	66·3	69·1
Standard deviation	8·9	—	3·9	2·5	3·8
1937					
Number of ramets	26	26	26	26	26
Flowering ramets	21	3	26	26	26
Maximum	41	10	58	64	63
Minimum	9	4	32	36	38
Mean	15·3	7·7	48·9	50·9	53·1
Standard deviation	—	—	7·6	6·3	6·0

Number of flowering stems per ramet.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
1936					
Number of ramets	26	26	26	26	26
Maximum	44	12	214	197	313
Minimum	12	0	65	49	40
Mean	23·5	3·7	116·5	115·7	150·1
Standard deviation	10·3	2·8	44·3	33·6	55·6
Total per soil	611	97	3028	3008	3902
1937					
Number of ramets	26	26	26	26	26
Maximum	11	3	192	278	326
Minimum	0	0	16	62	25
Mean	4·8	0·6	84·2	146·8	127·5
Standard deviation	2·8	0·9	47·8	59·5	78·7
Total per soil	125	15	2189	3818	3314

First flowering.

	1936					1937				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
13 July	—	—	—	—	—	—	—	1	—	—
14	—	—	—	1	—	—	—	10	12	4
15	—	—	—	1	—	—	—	15	12	7
16	—	—	—	1	—	—	—	16	14	10
17	—	—	20	10	5	—	—	16	16	11
18	—	—	23	13	5	—	—	16	17	11
19	—	—	23	13	5	1	—	24	25	24
20	—	—	23	13	5	1	—	—	25	24
21	1	—	23	13	5	1	—	—	25	25
22	1	—	26	25	15	6	—	—	25	25
23	2	1	—	26	26	6	—	—	25	25
24	2	2	—	—	—	7	—	—	26	26
25	3	2	—	—	—	9	—	—	—	—
26	3	2	—	—	—	10	—	—	—	—
27	3	2	—	—	—	11	—	—	—	—
28	11	2	—	—	—	13	—	—	—	—
29	11	2	—	—	—	15	—	—	—	—
30	11	2	—	—	—	15	—	—	—	—
31	11	4	—	—	—	16	1	—	—	—
1 Aug.	11	6	—	—	—	16	—	—	—	—
2	11	6	—	—	—	16	—	—	—	—
3	11	6	—	—	—	17	—	—	—	—
4	11	6	—	—	—	—	—	—	—	—
5	11	6	—	—	—	—	—	—	—	—
6	21	10	—	—	—	—	—	—	—	—
7	21	10	—	—	—	—	—	—	—	—
8	26	10	—	—	—	—	—	—	—	—
9	—	10	—	—	—	—	—	—	—	—
10	—	11	—	—	—	—	—	—	—	—

No more flowering occurred on any soil after 10 August 1936 and 31 July 1937.

Maximum primary florifery. For sand and calcareous sand 6. viii. 36; for clay, chalky clay, and Potterne soil 23. vii. 36. For all plots 21. vii. 37.

Fragaria vesca L.

Old stock. This was removed from the beds in March 1936. The final scorings for general tone (best first) and number of ramets surviving were: Potterne soil, 23 survivors; clay, 22 survivors; calcareous sand, 22 survivors; sand, 21 survivors; chalky clay, 8 survivors.

Redistribution experiments

Ramets from all soils were recloned from runners in the autumn of 1935. The new ramets were planted in the soils from which they were taken. Before transplanting on 13. iv. 36 the roots were washed to avoid the mixing of soils. The redistribution was so made that five ramets from every soil were transplanted on to every soil.

The ramets established themselves well. The only deaths were No. 49 (Aug. 1937), No. 141 (Sept. 1937), No. 57 (Dec. 1937). On chalky clay Nos. 77, 89, 90 showed considerable chlorosis (18. x. 37). First spring growth appeared

in early March 1937, the general order, most advanced first, was: clay, Potterne soil, sand, chalky clay, calcareous sand.

Seedlings.

	4. x. 36	24. xii. 36	9. iii. 37	23. vii. 37	17. x. 37	23. xii. 37
Sand	None	None	None	None	None	None
Calcareous sand	None	Few	None	None	Few	None
Clay	None	None	None	None	None	None
Chalky clay	None	None	None	None	Very numerous	Very few
Potterne soil	Very few	None	None	None	Numerous	None

The ramets flowered and fruited very irregularly in 1936.

Cloning of whole plant. Entire plants can be broken up into ramets and these established as successfully as from runners. No. 128 (from Potterne soil) was cloned in the autumn of 1935 and the ramets transplanted one each to every soil. General tone was scored as follows (best first):

6. vii. 36	22. ix. 36	10. v. 37	18. x. 37
Potterne soil	Potterne soil	Potterne soil	Potterne soil
Sand	Sand	Chalky clay	Chalky clay
Calcareous sand	Clay	Sand	Calcareous sand
Chalky clay	Calcareous sand	Clay	Sand
Clay	Chalky clay	Calcareous sand	Clay

	Runners 1936	Runners 1937	Fruiting stems 1937 (cm.)	First flowers 1937	First fruits 1937
Sand	28	22	11	16. v. 37	21. vi. 37
Calcareous sand	35	33	12	19. v. 37	23. vi. 37
Clay	34	22	15	16. v. 37	22. vi. 37
Chalky clay	28	39	11	16. v. 37	23. vi. 37
Potterne soil	37	34	22	11. v. 37	15. vi. 37

General tone for ramets on every soil taken as one sample. Sequence (best first):

30. v. 36	6. vii. 36	22. ix. 36	10. v. 37	6. vii. 37	18. x. 37
Potterne soil	Potterne soil	Potterne soil	Potterne soil	Potterne soil	Potterne soil
Chalky clay	Clay	Clay	Clay	Clay	Clay
Sand	Sand	Sand	Sand	Sand	Calcareous sand
Clay	Chalky clay	Calcareous sand	Calcareous sand	Calcareous sand	Sand
Calcareous sand	Calcareous sand	Chalky clay	Chalky clay	Chalky clay	Chalky clay

For equality of ramet size per plot (least deviation first): sand, calcareous sand, chalky clay, clay, Potterne soil (22. ix. 36). On 23. xii. 37 the same order was recorded, except that clay and Potterne soil had changed places.

Top hamper of fruiting stems decayed most quickly on clay and Potterne soil, though retained at least into mid-winter on all soils.

Partial "lifting" of the plants out of the soil was recorded, most first, on 23. xii. 37, in the following sequence: sand, calcareous sand, chalky clay, clay, Potterne soil.

General tone.

Now on	From ... Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Sand	(*a*) 1 (*b*) 3 (*c*) 3 (*d*) 3 (*e*) 3 (*f*) 3 (*g*) 16 (15)	(*a*) 5 (*b*) 5 (*c*) 5 (*d*) 4 (*e*) 4 (*f*) 2 (*g*) 25 (20)	(*a*) 3 (*b*) 2 (*c*) 1 (*d*) 1 (*e*) 2 (*f*) 4 (*g*) 13 (10)	(*a*) 2 (*b*) 1 (*c*) 4 (*d*) 5 (*e*) 5 (*f*) 5 (*g*) 22 (20)	(*a*) 4 (*b*) 4 (*c*) 2 (*d*) 2 (*e*) 1 (*f*) 1 (*g*) 14 (10)
Calcareous sand	(*a*) 2 (*b*) 3 (*c*) 3 (*d*) 3 (*e*) 3 (*f*) 3 (*g*) 17 (15)	(*a*) 5 (*b*) 4 (*c*) 4 (*d*) 4 (*e*) 5 (*f*) 4 (*g*) 26 (21)	(*a*) 1 (*b*) 1 (*c*) 1 (*d*) 1 (*e*) 1 (*f*) 1 (*g*) 6 (5)	(*a*) 3 (*b*) 5 (*c*) 5 (*d*) 5 (*e*) 4 (*f*) 5 (*g*) 27 (24)	(*a*) 4 (*b*) 2 (*c*) 2 (*d*) 2 (*e*) 2 (*f*) 2 (*g*) 14 (10)
Clay	(*a*) 2 (*b*) 3 (*c*) 3 (*d*) 3 (*e*) 3 (*f*) 3 (*g*) 17 (15)	(*a*) 5 (*b*) 5 (*c*) 4 (*d*) 4 (*e*) 4 (*f*) 4 (*g*) 26 (21)	(*a*) 3 (*b*) 1 (*c*) 1 (*d*) 1 (*e*) 1 (*f*) 1 (*g*) 8 (5)	(*a*) 1 (*b*) 4 (*c*) 5 (*d*) 5 (*e*) 5 (*f*) 5 (*g*) 25 (24)	(*a*) 4 (*b*) 2 (*c*) 2 (*d*) 2 (*e*) 2 (*f*) 2 (*g*) 14 (10)
Chalky clay	(*a*) 1 (*b*) 1 (*c*) 3 (*d*) 2 (*e*) 2 (*f*) 2 (*g*) 11 (10)	(*a*) 4 (*b*) 3 (*c*) 4 (*d*) 3 (*e*) 3 (*f*) 1 (*g*) 18 (14)	(*a*) 2 (*b*) 2 (*c*) 1 (*d*) 1 (*e*) 1 (*f*) 3 (*g*) 10 (8)	(*a*) 5 (*b*) 5 (*c*) 5 (*d*) 5 (*e*) 5 (*f*) 5 (*g*) 30 (25)	(*a*) 3 (*b*) 4 (*c*) 2 (*d*) 4 (*e*) 4 (*f*) 4 (*g*) 21 (18)
Potterne soil	(*a*) 4 (*b*) 4 (*c*) 4 (*d*) 5 (*e*) 4 (*f*) 4 (*g*) 25 (21)	(*a*) 3 (*b*) 3 (*c*) 3 (*d*) 2 (*e*) 3 (*f*) 3 (*g*) 17 (14)	(*a*) 2 (*b*) 1 (*c*) 1 (*d*) 1 (*e*) 1 (*f*) 1 (*g*) 7 (5)	(*a*) 1 (*b*) 5 (*c*) 5 (*d*) 4 (*e*) 5 (*f*) 5 (*g*) 25 (24)	(*a*) 5 (*b*) 2 (*c*) 2 (*d*) 3 (*e*) 2 (*f*) 2 (*g*) 16 (11)

Marks are awarded to groups of five ramets. These marks are relative only for the groups on the soil on which the ramets are now growing. 5 is best tone, 4 not so good, and so on. (*a*) 30. v. 36, (*b*) 6. vii. 36, (*c*) 22. ix. 36, (*d*) 10. v. 37, (*e*) 6. vii. 37, (*f*) 18. x. 37, (*g*) gives total values followed (in brackets) by total value less the first scoring.

The best result on all beds was with ramets which came from chalky clay, the next best with those from calcareous sand, followed by sand, Potterne soil, and (worst) clay.

Runners and fruiting stems. Total number of runners per ramet, (*a*) for 1936, (*b*) for 1937, and (*c*) mean height of fruiting stems for 1937.

Now on	From ... Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Sand	(*a*) 108 (*b*) 107 (*c*) 22·6	(*a*) 116 (*b*) 154 (*c*) 27·2	(*a*) 103 (*b*) 127 (*c*) 21·0	(*a*) 104 (*b*) 228 (*c*) 24·2	(*a*) 93 (*b*) 59 (*c*) 23·0
Calcareous sand	(*a*) 83 (*b*) 132 (*c*) 21·4	(*a*) 113 (*b*) 127 (*c*) 23·0	(*a*) 74 (*b*) 65 (*c*) 15·4	(*a*) 100 (*b*) 152 (*c*) 24·0	(*a*) 89 (*b*) 60 (*c*) 22·4
Clay	(*a*) 184 (*b*) 62 (*c*) 30·2	(*a*) 249 (*b*) 243 (*c*) 32·0	(*a*) 111 (*b*) 329 (*c*) 18·4	(*a*) 221 (*b*) 332 (*c*) 31·0	(*a*) 107 (*b*) 84 (*c*) 21·0
Chalky clay	(*a*) 64 (*b*) 117 (*c*) 18·4	(*a*) 83 (*b*) 69 (*c*) 22·4	(*a*) 74 (*b*) 58 (*c*) 18·6	(*a*) 80 (*b*) 95 (*c*) 23·6	(*a*) 100 (*b*) 181 (*c*) 22·4
Potterne soil	(*a*) 243 (*b*) 171 (*c*) 35·2	(*a*) 212 (*b*) 304 (*c*) 38·6	(*a*) 138 (*b*) 263 (*c*) 26·2	(*a*) 218 (*b*) 130 (*c*) 33·8	(*a*) 162 (*b*) 397 (*c*) 25·0

These figures give some support to the suggestion, from general tone, that the calcareous soils have an effect which is transmitted by cloning and maintained on other soils for the period of two years. This effect does not seem to be directly nutritional. It remains to be seen how long it persists.

Primary flowering (*a*) *and primary fruiting* (*b*) 1937.

The scheme below gives the mean first flowering date in May and the mean first fruiting date in June for 5 ramets:

Now on	From ... Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Sand	(*a*) 4·4 (*b*) 14·6	(*a*) 7·2 (*b*) 15·0	(*a*) 10·0 (*b*) 16·4	(*a*) 11·0 (*b*) 18·2	(*a*) 8·2 (*b*) 20·0
Calcareous sand	(*a*) 5·2 (*b*) 15·8	(*a*) 4·2 (*b*) 8·0	(*a*) 6·0 (*b*) 21·2	(*a*) 7·0 (*b*) 13·2	(*a*) 7·0 (*b*) 15·4
Clay	(*a*) 6·2 (*b*) 15·8	(*a*) 8·0 (*b*) 14·0	(*a*) 8·0 (*b*) 16·8	(*a*) 8·2 (*b*) 15·4	(*a*) 12·2 (*b*) 19·8
Chalky clay	(*a*) 8·4 (*b*) 14·2	(*a*) 7·0 (*b*) 18·0	(*a*) 10·0 (*b*) 18·2	(*a*) 5·4 (*b*) 14·4	(*a*) 9·0 (*b*) 17·2
Potterne soil	(*a*) 8·0 (*b*) 15·4	(*a*) 10·6 (*b*) 14·4	(*a*) 11·2 (*b*) 15·8	(*a*) 6·6 (*b*) 13·8	(*a*) 8·2 (*b*) 12·4

SUMMARY AND TENTATIVE CONCLUSIONS

1. Figures for rainfall, temperature and humidity are given for 1936 and 1937. There were no marked drought periods either year. Soil temperatures were taken at frequent intervals throughout the two years.

2. The results of periodic records of the six species now in position for the two years 1936 and 1937 are embodied in this report. The chief facts which have emerged are:

Centaurea nemoralis. This species continues to maintain itself as a persistent perennial. Three additional deaths have occurred, two on clay and one on Potterne soil. No deaths have so far been recorded on either of the sands. No morphological differences between the ramets on the different soils have appeared. The habit differences between the ramets (of one and the same clone) at Kew (stems widely ascending) and Potterne (stems erect) have been maintained for ten years. The general tone was best and the number of flowering stems was highest on the sands. The total number and mean per ramet of flowering stems showed a further decrease from 1935 to 1936 for all soils except chalky clay, but a surprising rise for all soils from 1936 to 1937. Since this species has been in position from the beginning of the experiments it is important to note that the 1937 results do not suggest signs of soil exhaustion.

Silene maritima. A standard description is given of the new stock. The narrow-leaved variety used (as a single clone) showed no habit or morphological differences on the different soils except for a possible very slight relative decrease of leaf size on the sands. There was no change of deep anthocyanin content or narrow-cylindric calyx on any soil. This stock appears to be much less plastic than the stock used in earlier experiments. Thirteen deaths have occurred on the sand, all in spring and summer 1937; no deaths on the other soils have been recorded. The general tone has become moderately stabilized as best on Potterne soil, intermediate on clays, and worst on sands. The same sequence is shown for ramet diameters, measured from branch ends. Seed

production was small and seedlings were relatively few, because the stock produces large numbers of purely female flowers.

Plantago major. A standard description is given of the new stock. This, in contrast with the material used in earlier experiments, is a tall large-leaved variety. Only two deaths occurred, both in 1937, one on calcareous sand and one on sand. The general tone has become fairly stabilized as best on Potterne soil, intermediate on the clays and worst on the sands. Ramet diameter, except on chalky clay, where it has slightly fluctuated, gave the same sequence. Length and breadth of the largest leaves per ramet also showed the same order, as does also, for 1937, the number of flowering spikes, but number of crowns was highest on clay, both per ramet and total per soil. The height of flowering stems varied from 1936 to 1937. In the latter year it was greatest on chalky clay and lowest on calcareous sand. Differences in habit (flat to strict) occurred in this stock as in that previously used. On the whole the flat habit predominates on the sands and is correlated with smaller size and fewer leaves, and the more or less strict habit predominates on the clays and Potterne soil and is correlated with larger size and more numerous leaves.

Phleum pratense has survived without further deaths on any soil. The general tone has kept uniform in the following sequence (best first): Potterne soil, clay, chalky clay, sand, calcareous sand. Seed germination was again best on Potterne soil and sand, and attained maxima in spring and autumn. Maximum height of flowering stems and number of flowering stems (total per soil and mean per ramet) has been greatest on Potterne soil, lowest on sands, and intermediate on clays. Numbers of flowering stems and their mean maximum heights decreased on all soils from 1936 to 1937. This result is the reverse of that for *Centaurea nemoralis*.

Phleum nodosum. No deaths have occurred on any of the soils. The general tone was best on Potterne soil, intermediate on the clays, and worst on the sands. The mean maximum heights of flowering stems was greatest on Potterne soil, lowest on the sands, and intermediate on the clays for both years. The number of flowering stems was lowest for both years on the sands but there was fluctuation for highest number between chalky clay and Potterne soil. The low total numbers on the sands, and especially on calcareous sand is remarkable. In 1937 many ramets did not flower at all and a considerable number did not make any attempt to produce flowering stems.

Fragaria vesca. Ramets from all soils were recloned in 1935 and transplanted on to all soils in April 1936. The general tone for all ramets, contrasted soil against soil, has become fairly stabilized as follows (best first): Potterne soil, clay, sands, chalky clay. For groups of ramets from different soils the results show that those from chalky clay were best, followed by those from calcareous sand, followed by sand, Potterne soil, and (worst) clay. Similar, though rather less marked, results were obtained by analysing the counts of runners and measurements of stem heights. It appears that the calcium

carbonate in some way acts as a favourable stimulus to growth, the influence being marked for at least two years. Flowering and fruiting were too irregular, with the small numbers in the samples, to give any clear indication of the effect of soils.

3. Moss growth and slug attack were both greater in the wetter seasons 1936 and 1937 than in 1934 and 1935.

4. Primary flowering has again been carefully recorded. *Centaurea nemoralis* showed little difference between 1936 and 1937 but was very slightly earlier in the latter year. *Silene maritima* was remarkable for the quick completion of first flowering by all ramets on sand and chalky clay as contrasted with the slow completion by ramets on calcareous sand and Potterne soil. First flowering of *Plantago major* showed scarcely significant fluctuations for the two years and from soil to soil. It was most long drawn out and last to complete on clay in 1936 and last to commence on clay in 1937. Primary flowering commenced and was completed in the very short space of 7 days in 1936 and 4 days in 1937 on all soils in *Phleum pratense*. The poverty of flowering stem production on the sands in *P. nodosum* caused delayed or incomplete flowering. Primary flowering for this species showed no significant differences for the clays and Potterne soil, as between the soils or for either year.

5. A summary of the results of these experiments as they have been carried out during the past ten years follows as a separate paper.

TRANSPLANT EXPERIMENTS OF THE BRITISH ECOLOGICAL SOCIETY AT POTTERNE, WILTSHIRE

SUMMARY OF RESULTS, 1928–37

By ERIC M. MARSDEN-JONES and W. B. TURRILL

I. Introduction

The Transplant Experiments at Potterne were commenced, after preliminary investigations, in the spring of 1928. Five biennial reports have been prepared and published as follows:

I. This *Journ.* **18**, 352–78 (1930).
II. ,, **21**, 268–93 (1933).
III. ,, **23**, 443–69 (1935).
IV. ,, **25**, 189–212 (1937).
V. ,, **26**, 359–79 (1938).

In the following summary these papers will, where it is necessary to quote them, be referred to by the numbers I, II, III, IV, and V respectively.

The experiments were designed "to determine the effects of different soils on selected species of the British flora" (I). Four "soils" were imported, namely, sand, calcareous sand, clay, and chalky clay. Beds on the Potterne Upper Greensand soil (*in situ*) were used as controls. Details of origin and analyses of the original soil materials were given (I, pp. 353–4). The four "soils" were imported into strong wooden enclosures 3 ft. deep, 35 ft. long, 10 ft. broad, with 6 in. of cinders at the bottom. Each "soil" was divided into 6 "beds", 10 ft. × 4 ft. 9 in., separated by narrow paths. With a few exceptions, 26 individual plants were spaced out on every "bed". Every plant was labelled with a permanent number.

The species used in the ten years, with dates, are:

Centaurea nemoralis Jord. "forma *radiata albiflora*" 1928–37 (ramets used).
Silene vulgaris Garcke 1928–31 (seedlings used).
Silene maritima L. 1928–33 (seedlings used).
Anthyllis vulneraria L. 1928–30, 1930–33, 1933–5 (seedlings used).
Plantago major L. small var. 1929–35 (seedlings and ramets used).
Fragaria vesca L. 1932–7 (ramets used).
Phleum pratense L. 1932–7 (ramets used).
Phleum nodosum L. 1932–7 (ramets used).
Plantago major L. large var. 1936–7 (ramets used).
Silene maritima L. narrow-leaved var. 1936–7 (ramets used).

II. METEOROLOGICAL CONDITIONS

Self-recording instruments were installed in the spring of 1929 and regular records for temperature, humidity, and rainfall have been kept since that date, with the exception of a few brief periods. The data for 1928 and 1929 are from another local source. The rainfall totals are:

1928.	666·5 mm. = 26·66 in.	1933.	543·6 mm. = 21·74 in.
1929.	663·75 mm. = 26·55 in.	1934.	600·75 mm. = 24·03 in.
1930.	761·1 mm. = 30·8 in.	1935.	843·75 mm. = 33·75 in.
1931.	708·6 mm. = 28·4 in.	1936.	712·5 mm. = 28·5 in.
1932.	733·25 mm. = 29·3 in.	1937.	828·0 mm. = 33·12 in.

1928 had a low total rainfall, frosts in April, May, and September, but a mild October and November.

1929 was remarkable for a hot dry summer and a wet autumn and winter, but a low total rainfall.

1930 and 1931 were characterized by the absence of any long dry summer period and by the occurrence of cold spells in spring.

1932 was noteworthy for a spell of seven continuous weeks in January and February with no "rain days" and irregular rainfall during the rest of the year, with no long dry summer period.

1933 was remarkable for the low total annual rainfall and a hot spell from June to August.

1934 had an early summer drought in May and June.

1935 showed a summer drought in July and the first fortnight of August. A very late frost affected many plants on 16 May from 12 midnight to 7 a.m.

1936 showed relatively dry periods in May and August, but no prolonged period of hot drought.

1937 had relatively dry spells at midsummer and in November.

Weather conditions affected the experiments in several ways:

(1) Through the soils—in wet weather puddling the clays, in dry weather making the clay powdery, aggregating the chalky clay in hard small lumps, and making the surface of the sands and Potterne soil loose and dust-like.

(2) Directly on the plants: (*a*) drought has caused wilting in *Fragaria* on Potterne soil, deaths of *Silene maritima* on sand only, "burning" of leaves and shoots in *Phleum nodosum* on all soils, and reduced or retarded the production of flowering stems in *P. nodosum*, especially on sand and chalky clay; (*b*) excessive wet has caused rotting of crowns in *Silene vulgaris* on clays, damping off of *S. maritima* seedlings, especially on clay, and lodging of flowering stems in *Phleum pratense* on Potterne soil; (*c*) frost has caused deaths of *Anthyllis* plants on sand, clay, and Potterne soil, lifting of plants of *Plantago major*, especially on sands, clay, and Potterne soil, lifting of *Anthyllis* seedlings on all soils, and late frost caused "black-eye" in *Fragaria* on Potterne soil; (*d*) cold

winds killed young foliage of *Centaurea* on all soils and caused lodging of stems in *Centaurea* on sand.

(3) Indirectly by modifying biotic factors: (*a*) by excessive wet increasing and drought decreasing slug populations. Slugs were at least partly responsible for a high death rate in *Silene maritima*, especially on the clays, after much wet, and for damage to *Centaurea* on clay and *Plantago* on chalky clay; (*b*) by excessive wet causing an increase in fungus diseases, as *Marssonina* on *Silene* spp. and *Ramularia* on *Plantago*.

(4) Through plants acting on the plants—good growing conditions cause the development of much "top hamper" and certain plants, especially those in central rows, tend to be smothered out, as is well shown on some *Centaurea* beds.

III. Biotic factors

Mosses. In the winter of 1929–30 mosses appeared in some abundance on the undisturbed parts of the beds not occupied or shaded by plants. They have persisted with varying frequencies since, especially after wet seasons, on calcareous sand and sand. It is noteworthy that *Ceratodon purpureus* was one of the most abundant species on the non-calcareous soils, but has not been recorded on the calcareous soils. *Barbula* spp. were abundant, except on sand. *Funaria hygrometrica* died out quickly. *Dicranella heteromalla* and *Fissidens taxifolius* are late arrivals.

Lichens. Cladonia sp. appeared in 1931 on sand as two small patches and has since spread greatly, but has not been recorded for other soils.

Slugs. These were first noted in June 1931. After wet seasons, especially on the clays, they did considerable damage, and preventive measures had to be taken against their increase.

Worms. On chalky clay and calcareous sand worm action produced marked "heaping up" of small stones.

Grasshoppers. Small grasshoppers[1] [*Chorthippus* (*Stauroderus*) *bicolor* (L.)] appeared first on Potterne soil, where they remained most abundant. They have been entirely limited to the clumps of *Phleum nodosum*.

Miscellaneous. Local and temporary occurrences of the following have been noted: long-tailed field-mouse (on calcareous sand), moles (*Centaürea* plot on Potterne soil), wireworms (Potterne soil, only for a time after removal of turf to make the beds), and black-fly (on *Centaurea*, on sand, cleared by *Coccinella* larvae).

[1] Kindly determined by C. Diver, who informs us that this species is a regular inhabitant of grasslands and one of the common species in this country. It is generally a "dry" species, but tolerates a certain amount of marshiness, as is shown by its distribution at South Haven Peninsula (*J. Anim. Ecol.* **2**, 58).

IV. SPECIES

Centaurea nemoralis. This species has proved a persistent perennial and does well on all the soils, but best on the sand and a little less well on calcareous sand. It is the only species which has done best on the sands. No morphological changes have occurred at Potterne. The growth of basal and lower cauline leaves on the clay and Potterne soil is relatively retarded so that spring shoots retain arachnoid indumentum for a longer period than on other soils. Many ramets now show "fairy-ring" growth and natural recloning. At Kew control ramets of the same clone speedily developed widely ascending flowering stems, while at Potterne on all soils the flowering stems were erect. This difference has been maintained through the ten years. The results of the 1937 scoring do not suggest any sign of soil exhaustion. (References: I, 356; II, 272; III, 446; IV, 192; V, 363.)

Silene vulgaris. After considerable fluctuation the best tone was constantly on chalky clay and the worst, nearly constantly, on sand. No fixed habit or other morphological changes have been recorded on any soils for the aerial parts. In 1928–9 plants on calcareous sand tended to develop a strict habit of growth, this, however, became much less marked in 1930 and had almost disappeared in 1931. On clay the plants developed and retained a yellowish green colour. On clay the main roots spread nearly horizontally. On the remaining soils they penetrated nearly vertically, but were much coiled immediately below the root-stock on the Potterne soil. The superficial cells of the older roots were coloured differently in the various soils and the roots showed important anatomical differences (see Millner, *New Phytol.* **33**, 77, 1934). The species behaved as a hemicryptophyte on all soils. (References: I, 360; II, 274.)

Silene maritima. The first year (1928) the plants were best on Potterne soil and worst in general tone on calcareous sand. A complete reversal gradually became established and in 1931 living plants on calcareous sand were best, on chalky clay worst, and on Potterne soil all the plants had died. Habit changes appeared on the different soils. On the sand the plants had a flat habit, relatively small leaves, and a greater amount of anthocyanin. On calcareous sand the leaves were also smaller than in the original parent. On clay the plants became decidedly woody as their age increased. Plants on all soils showed rooting at the nodes. On clay many main roots spread horizontally a short distance below the surface. On the sand and calcareous sand the roots penetrated nearly vertically. On the Potterne soil they were much coiled immediately below the root-stock. The superficial cells of the older roots were coloured differently in the various soils. It is unfortunate that the death rates of this and the previous species were so high. The results obtained, with *S. maritima* especially, suggested that if the plants had continued alive

interesting and marked morphological changes would have occurred. (References: I, 364; II, 278; III, 450; IV, 196.)

Anthyllis vulneraria. No morphological changes of a qualitative nature occurred in three generations of seedlings of selfed origin. Tone fluctuated considerably, but at first the seedlings generally did best on Potterne soil, but at the maximum flowering period the general vigour, growth, and health were best on the calcareous soils. Plants in isolated cultivation often show very luxuriant growth, with abundant flower and seed production, which appears to make them more susceptible to fungus parasites (*Verticillium,* etc.) attacking roots and crowns. Under natural grassland or pasture conditions competition with other vegetation and grazing by rabbits and sheep reduce luxuriance of growth and, especially the natural pruning by grazing, tend to "harden" the plants and thus to increase survival. Unlike some varieties of *Anthyllis,* that used on the Transplants is highly self-fertile. Root nodule development was lowest for number on clay, and for size on sand. On other soils there was considerable fluctuation. The better general tone of the plants on plots new to *Anthyllis* compared with material grown on soils cropped with *Anthyllis* for six consecutive years suggested soil exhaustion or a "sick soil" factor. Chemical analyses of plants grown on the five soils showed a high percentage of calcium in the ash of plants grown in the sand—a soil which contained no determinable calcium carbonate when analysed at the commencement of the experiments. (References: I, 369; II, 282; III, 451; IV, 196.)

Plantago major, small variety. The particular interest of the experiments with this plant is the considerable change, especially in size, produced very quickly by growing on different soils. *P. major* is exceedingly plastic. The dwarf habit of the original stock was approximately retained on the sands. Plants on clay and Potterne soil within a few months became large and luxuriant in growth. Marked differences in size appeared in seedlings within one month of sowing seed on the five soils. Persistence of plants was most marked on clay. On the sands and Potterne soil the peduncles produced spreading hairs; on the clays the peduncles were glabrescent below and had adpressed hairs on the upper part. Peculiar fluctuations between a strict and flat habit appeared first on the calcareous soils and later on the non-calcareous soils. At present no explanation of the peculiar fluctuation often of one and the same plant, or even one rosette of a plant, between the strict and flat habit is forthcoming. The extreme conditions are so strikingly different that they could not be ignored. There seems to be no significant correlation between these habit fluctuations and age, season, or soil.

Plants which had been six years growing on the clay and which had become large and luxuriant in growth were cloned and the ramets distributed over all the soils. There was no indication of the transmission of edaphic influence causing relative gigantism on the clay beyond a first brief period of growth. A year after redistribution, Potterne soil and clay were nearly equivalent for all

the scored characters, and there was a very large qualitative and quantitative gap between the plants on these and those on chalky clay, which finally occupied the third place and showed chlorosis. The plants on the sands had reverted to a dwarf habit. The figures for size and counts of flowering spikes were lower for all soils than the figures for the original plants on the respective soils; had there been any transmission they should have been higher (except on clay). (References: I, 372; II, 286; III, 454; IV, 198.)

Fragaria vesca. The ramets have done best in general tone and number of runners produced on Potterne soil and clay and worst on chalky clay. Chlorosis was strongly and increasingly shown on the chalky clay, but not on the calcareous sand. Runners were removed and counted several times a year from all plants except four per soil. Plants from which runners were removed developed new runners which were stouter than those of plants from which runners were not removed. The ramets from which runners were removed were, during the first two years, larger and had more leaves than ramets which were allowed to runner freely. The early summer drought of 1934 adversely affected the ramets in their third year and was one cause of the decrease in heights of fruiting stems and in numbers of runners. Contributory causes were increasing "old age" of the ramets in one position and the cumulative effects of adverse soil conditions on chalky clay and the sands. All the observations, qualitative and quantitative, indicate that *Fragaria* flourishes best, over a period of years, when allowed to occupy fresh ground by means of runners. Slight differences in the taste of mature fruits from the different soils were recorded.

In 1936 ramets, recloned from ramets growing on all soils, were transplanted on to all soils. The general tone was speedily re-established as best on Potterne soil and clay and worst on chalky clay. Analysis of the groups of ramets from different soils showed that those from chalky clay were best, followed by those from calcareous sand, sand, Potterne soil, and (worst) clay. It appears that the calcareous soils have an effect which is transmitted by cloning and maintained on other soils for the period of two years. Since plants growing on chalky clay in the first experiment (of 4 years' duration) did badly for all characters it seems probable that the effect of calcium carbonate on ramets moved to other soils is not directly nutritional. It remains to be seen how long the effect persists. (References: I, 375; III, 458; IV, 203; V, 374.)

Phleum pratense. This species has survived well on all soils. Very considerable differences in quantitative characters appeared early between the ramets on the different soils. These differences have progressively increased. They are shown by general tone, maximum height of flowering stems, and number of flowering stems. The maintained sequence has been best or highest on Potterne soil, worst or lowest on the sands, and intermediate on the clays. A slight indication of soil exhaustion or "sick-soil" effects appeared from 1936 to 1937. (References: III, 462, 465; IV, 208; V, 371.)

Phleum nodosum. This species has survived well on all soils. Very considerable differences in quantitative and qualitative characters appeared early between the ramets on the different soils. These differences have progressively increased. They are shown by the general tone and maximum height of flowering stems, in part rather less by number of flowering stems. The maintained sequence has been best or highest (except for fluctuation in number of flowering stems) on Potterne soil, worst or lowest on the sands, and intermediate on the clays. The low numbers of flowering stems in 1936 and 1937 on the sands were remarkable. (References: III, 462, 463; IV, 206; V, 373.)

Plantago major, large variety. Genetically tested stock of a large-leaved variety was included in the experiments in 1936. It was deliberately selected as showing marked contrasts with the dwarf small-leaved variety previously used. Like the latter it proved exceedingly plastic, but the changes occurred in a reverse direction, i.e. instead of small plants becoming relatively large on clay and Potterne soil, large plants became small on the sands. Within two years the general tone became fairly stabilized as best on Potterne soil, intermediate on the clays, and worst on the sands. Ramet diameter, length and breadth of the largest leaves per ramet, and number of flowering spikes showed the same general sequence, but the number of crowns was highest on clay. Fluctuations from a flat to a strict habit occurred also in this stock. On the whole, the flat habit predominated on the sands and was correlated with smaller size of the plants and fewer leaves per ramet; the more or less strict habit predominated on the clays and Potterne soil and was correlated with larger size of the plants and more numerous leaves per ramet. (Reference: V, 367.)

Silene maritima, narrow-leaved variety. This has been in position only two years. The general tone has become moderately stabilized as best on Potterne soil, intermediate on clays, and worst on sands. The same sequence is shown for ramet diameters. No morphological differences have appeared on the different soils, except for a possible very slight relative decrease of leaf size on the sands. There was no change of deep anthocyanin content or narrow-cylindric calyx. This stock appears, at present, to be much less plastic than the stock of the same species used earlier in the experiments. (Reference: V, 364.)

V. Deaths and survivals

Early in the experiments it became obvious that the death rate might vary very considerably from species to species and from soil to soil. Careful records of all deaths were therefore kept. The following briefly summarizes the results:

(i) Persistent species, with relatively low mortality on all soils, *Centaurea nemoralis*, *Phleum nodosum*, and *P. pratense.*

(ii) Species with significantly different death and survival rates on different soils, *Silene vulgaris* (survived best on calcareous sand, highest death rates on clays and Potterne soil), *S. maritima* (survived best on the sands, highest death

rates on Potterne soil and clays), *Anthyllis vulneraria* (best survival on chalky clay), *Fragaria vesca* (highest death rate on chalky clay), *Plantago major*, small var. (survived best on clay).

(iii) The causes of death were varied. They included: drought, frost (including "heaving-out"), fungus disease (especially root-damaging fungi), slugs, wireworms (on Potterne soil only, early after removal of turf), smother effects of top hamper, and chlorosis (on chalky clay).

VI. SEEDLINGS

All or some of the plants have been allowed to seed and full records of seed germination on the different soils have been made. It was, of course, impossible to allow the seedlings to become established. The following are the generalized results:

Centaurea nemoralis. Best germination on sands and in spring, some years also in autumn.

Silene vulgaris. Spring germination. Irregular on different soils.

Silene maritima. Autumn and spring germination. Irregular on different soils.

Anthyllis vulneraria. Continuous germination, except in frost, especially in spring and autumn. Irregular on different soils.

Plantago major. Continuous germination, mainly spring and early summer; best on Potterne soil. Seeds over-winter in the infructescences.

Fragaria vesca. There is immediate and also delayed germination, and germination may be continuous through summer and autumn. Germination is best on Potterne soil.

Phleum pratense. Mainly spring and autumn germination. Now numerous on all soils.

Phleum nodosum. The clone is completely self-sterile.

VII. PHENOLOGY

General records of the phenological behaviour of vegetative parts and full detailed records for first flowering of all ramets have been kept. The latter may be briefly summarized as follows:

(i) Three important sets of variables have to be taken into account: the species, the soils, the weather from year to year.

(ii) *Centaurea nemoralis*. No constant significant differences between the soils. Early drought and late frosts have retarded flowering.

Silene vulgaris. Earlier flowering on calcareous sand and later flowering on Potterne soil.

Silene maritima. Earlier flowering on calcareous sand and later flowering on Potterne soil. Primary flowering commences earlier in *S. maritima* than in *S. vulgaris*.

Anthyllis vulneraria. Earlier flowering on calcareous sand.

Plantago major, small var. Earlier completion of first flowering on clay and long delayed completion on sands. This is simply correlated with abundance of flowering spikes.

Fragaria vesca. No constant significant differences between the soils. Early drought retarded flowering and fruiting.

Phleum pratense. No constant significant differences between the soils. Early drought and late frosts have retarded flowering.

Phleum nodosum. No constant significant difference between the soils or with weather conditions. The period of primary flowering tends to be increasingly long drawn out owing to poor development of flowering spikes on the sands.

VIII. General results

While the experiments were started with a completely open mind and have been conducted without bias towards any particular evolutionary or other theories, the possibility of mutations arising or of perpetuation of effects has, of course, been kept in mind. Neither have mutations occurred nor (with the possible exception of the "stimulus" effect of chalky clay on *Fragaria*) have long sustained effects of different edaphic conditions been recorded after re-transplanting. Two species pairs have been used, namely, *Silene vulgaris* and *S. maritima*, and *Phleum pratense* and *P. nodosum*. No one of these four species showed on any soil morphological changes which made it more like its congener. Changes of a parallel nature were shown by the members of each pair.

So far as reactions to edaphic conditions are concerned every species is "a law unto itself", in the sense that it is impossible to foretell, without experiment, what will be its reaction to any combination of soil factors. Even ramets have a certain "individuality". The least plastic species (under varying soil conditions) so far tested in the experiments are *Centaurea nemoralis* and *Anthyllis vulneraria*. The most plastic species used is *Plantago major*. This applies, in a reverse manner, both to the small-leaved and the large-leaved varieties.

There is no doubt that different soils have, with certain species, a selective effect. This is shown by differential death rates, greater or less growth vigour, different number of flowers produced, and different seed germination. High death rates have sometimes interfered with other aspects of the experiments.

On the whole the species tested have made most growth and have produced most flowers and fruits on Potterne soil and clay. They have made least growth and have produced fewest flowers and fruits on sand. There are, however, exceptions to this generalization. Thus, the position for *Centaurea nemoralis* is exactly the reverse. Analyses (I, 354) showed that clay and Potterne soil were more alike chemically than any other two of the "soils" used. The clay was slightly alkaline and the Potterne soil slightly acid (as

collected). The two soils are physically very different. The sand was found to be markedly deficient in "available" phosphorus, "available" potassium, and in calcium carbonate.

The intention of the committee has been to study the influence of edaphic factors on selected species, keeping all other factors uniform, and the general conditions as natural as possible. This is an impossible ideal under conditions of transplant experiments in large open enclosures. It has been found that even when the soils are transported to one locality, so that the weather and climatic factors are the same for all the enclosures, there is still a complicated interaction between the groups of factors usually referred to as climatic, edaphic, and biotic. Thus seasonal weather acts on the plants differently through the different soils, while biotic factors, such as slugs, vary in the intensity of their action on the plants with both soils and weather. The soil factor is itself a complex of varying physical and chemical characters. Conditions, other than soils, have, of course, been kept as uniform or as equally distributed as possible, but only a degree of precise control can be attained much below that of laboratory experiments.

As there was no previous experience of experiments of similar nature to those summarized above, new technique and methods had to be devised and tested. Some had to be modified, some completely dropped or changed, and some new ones introduced as the experiments progressed. So far, only perennial herbs have been used, and in their choice there was a considerable element of chance, except that species were selected that appeared to be easy to transplant and to keep as individuals and concerning which a certain amount was known, or could within reasonable time be discovered, about their genetical behaviour. In recording the structure and behaviour of the plants themselves both "qualitative" and "quantitative" characters were utilized. There had to be a selection of these based on a gradually increasing experience. On the whole, those characters have, it is felt, been selected which best express soil influences.

GROWTH AND SURVIVAL OF PLANTS IN THE ARCTIC

By HAROLD G. WAGER

(*With Plates V and VI, and one Figure in the Text*)

Introduction

Certain types of arctic and alpine climates tend to allow the development of open associations of plants, which have been called "fjaeldmark" by Warming. In these associations the adults live for a great length of time and appear to be healthy and grow to a large size, often producing abundant flowers and fertile seeds. It is clear that the climate is such that the plant species can flourish, so it is curious that in the course of time these areas should not have developed a closed association. The work to be described was done in an endeavour to obtain some evidence of the factors responsible for this state of affairs.

Warming (1909) states that "fjaeldmark" develops wherever the temperature of the warmest month does not exceed 6° C., and further says "that there is evidently some connexion between the temperature and the density of the vegetation". Such statements are of a purely descriptive nature and are obviously only true given a large number of other suitable environmental factors.

In 1932 I spent the summer on the east coast of Greenland,[1] and noticed that in the "fjaeldmark" there appeared to be a large number of seedlings and young plants present in comparison with the number of adults, and concluded that the factor preventing further colonization might be found in some condition which was damaging to the survival of seedlings.

During a year[2] spent in East Greenland at Kangerdlugssuak (lat. 68° 30′) I collected data on this question of seedling survival and growth rate in an endeavour to find the causes producing the static open association of the "fjaeldmark".

A general point with regard to the colonization of the "fjaeldmark" in the area investigated is that there is no preliminary growth of lichens and mosses before that of the flowering plants. Where no flowering plants are growing the earth surface is bare, and mosses are not common except near streams, or in places where the soil is very wet in the spring and early summer. Lichens are almost restricted to small encrusting forms on the larger stones. These observations apply both to the coastal regions and also to the Nunataks far inland near to the ice cap. Hence questions of competition with lower plants do not arise.

[1] The writer was included, as a geological assistant, in the Scoresby Sound Committee's Second East Greenland Expedition (1932) under the leadership of Capt. Einar Mikkelsen, and for this he desires to express his indebtedness.

[2] The work described in this paper was carried out on the British East Greenland Expedition 1935–6 under the leadership of L. R. Wager. A general account of this expedition and the work done on it has been published (Wager, 1937).

In the district examined, the vegetation varies from a completely closed herb field association to barren land. These extremes are often found in close juxtaposition and appear to be fairly stable. In the writer's opinion a distinction must be made between areas which have suitable soil conditions for plants, i.e. presence of moisture, soil stability, soil particle size, etc., and those which cannot be colonized because of unsuitable soil conditions. In the present account "fjaeldmark" is only being used to describe the former type of area.

The question arises as to whether the sequence from bare earth to a closed association is a continuous one or whether there is a fairly abrupt change from the one to the other at some stage of environmental suitability for plant growth. In the writer's opinion this change is fairly abrupt and "fjaeldmark" does not drift by small changes into a closed association. It follows from this that it is believed that "fjaeldmark" is a definite vegetation type and not simply an intermediate stage from herb field to bare earth. In the part of the coast surrounding Kangerdlugssuak it is characteristic of large areas and it extends inland to the edge of the ice cap.

METHOD OF STUDY

During a single year it is impossible to carry out controlled experiments on growth and survival, and so, instead, the study of the population already growing was undertaken.

Areas of "fjaeldmark" were selected and on them quadrats were set out and mapped as soon as possible after arrival, unfortunately not till 8–15 September 1935. These quadrats were remapped, some between 5 and 12 July and others between 15 and 17 August 1936. In this way it was hoped to trace the individuals over the period of a year and hence to determine at what age the plants were most susceptible to their environment. Unfortunately, the scheme did not work well, as it was found, when the quadrats were remapped, that many of the small plants had been missed in the autumn, particularly those species with leaves which dried up and shrivelled back so that they could be hidden by small pebbles. Further, the accuracy of the mapping of the plants in the more dense quadrats was not sufficiently great to allow more than about 70 % of the individuals to be traced with certainty. This was the result of the conditions of the autumn work, poorish light, and rather severe weather for detailed outdoor studies. As a result the only reliable maps of most of the quadrats are those of the summer of 1936.

The distribution of plants in the quadrat maps show that there is a tendency for young plants to be grouped round a flowering adult, presumably because of the density of seeding, but that there is no noticeable tendency to get a development of young adults in that position. This means that tufts of vegetation are not being produced. The general appearance and type of

earth surface of a typical quadrat is shown by the photograph of quadrat 4 (Pl. VB). It is seen that the earth surface is a mixture of stones of very varied sizes and fine earth such as is characteristic of the more stable parts of moraines. The only plant that can be seen is the single adult of *Luzula spicata* which had produced seeds for many years, as may be seen by the dried up remains of flowers attached to the plant. The remaining plants, 120 in all, are too small to be seen, as none exceed an inch in height.

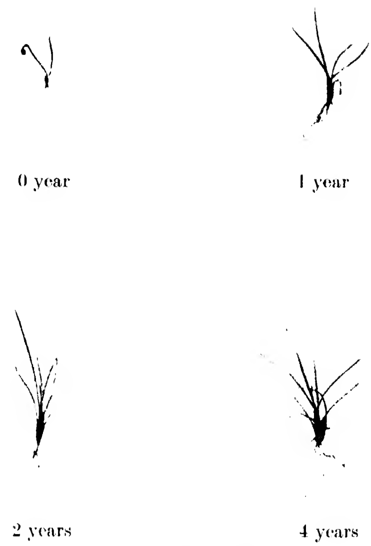
Plants in the Arctic grow extremely slowly, as will be apparent from the sizes and weights given later, and, in consequence, it was possible to distinguish the following eight age groups, 0 year, 1 year, 2 year, ..., 5 year, "*a*", "*A*". The "0" year plants were those grown from seed in the current year; the "1" year were plants in their second year, etc. "*a*" plants were larger than the "5" year class, yet still small and generally non-flowering, with ages varying from about 5 to 10 years; "*A*" were those plants that could be called adult and flowered freely. These various age groups were used in entering the plants on the quadrat sheets.

As this work depends on the accuracy of the assessment of the age of the plants, a fairly detailed statement of the methods of distinction between the different ages must be given. The various species mapped will be considered separately, but certain general points may be made first.

The difficulty of judging the age increases progressively with the age of the plant, because the divergence of the individual from the average due to minor environmental fluctuations increases. The age of those species such as the grasses and *Luzula*, which have leaves which do not shrivel on death to any great extent and which decay very slowly, are the easiest to determine, and a species such as *Salix* in which the leaves are shed is probably the most difficult.

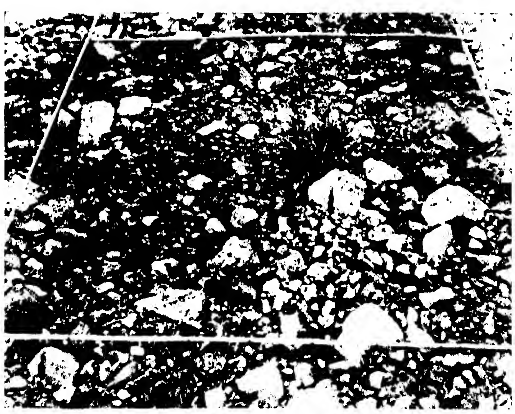
The criteria outlined below are the result of the study of young plants growing not only in the "fjaeldmark", but also in other localities as well, in autumn and in the spring and summer. In the late spring when all the leaves are formed it is easy, in the large populations available for study, to build up the criteria for age determination, starting from the "0" year plants, which are unmistakable, and passing to the "1" year plants with dead leaves corresponding to the "0" year ones, and so on through four or five years. It is obvious that mistakes will be made, but by dealing with large numbers, some 2000 plants were mapped twice over, these will tend to average out. A check on the accuracy of the age determinations was obtained when the same plants were mapped in the second year, as it was found that the new ages assigned corresponded to those of the previous year in a very large proportion of the cases.[1]

[1] The dimensions and photographs of plants given in this section and the weights given in a subsequent one were obtained from a series of plants collected adjacent to the quadrats and their ages were determined at the time of collection and so correspond to those used on the quadrat sheets.



A. *Luzula spicata.*

The plants are reproduced natural size.



B. Appearance of a typical quadrat (see p. 392).

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Face p. 392

The "0" year plants were identified by the presence of functional seed leaves in the case of the dicotyledons, and in the case of the grasses and *Luzula* by the presence of the seed coat or glumes and by the absence of dead leaves.

Luzula spicata (Pl. V A)

The age may be determined by the total number of leaves present, both living and dead. Two, or less frequently three, leaves are produced in the first year; in the second year two or three more leaves are produced. The third year plant may have two to four living leaves and four to six dead ones, and the fourth year plant grows three to five leaves. The "4" and "5" year groups are decided by judgment, mainly by the size, as some of the earlier leaves may have rotted away by then. There is generally no lateral branching in the "5" year plants. The approximate sizes of the plants are as follows:

"0" year, 0·6 cm.; "1" year, 0·7 cm.; "2" year, 2·1 cm.; "4" year, 1·8 cm.

Grass

The species of grass mapped was in most cases *Trisetum spicatum* but in quadrat 12 it was mainly *Phippsia algida*. The criteria of age are the same as for *Luzula* except that the number of leaves produced in any year tends to be the smaller of the two figures given, and even in some cases only three leaves are present by the end of the second year and five or six by the end of the third year, and so on. A rough average for the length of the longest leaf of plants of the various ages is given below:

"0" year, 1·0 cm.; "1" year, 1·2 cm.; "2" year, 1·7 cm.; "3" year, 1·6 cm.; "4" year, 2·3 cm.

Oxyria digyna (Pl. VI B)

The age groups are judged partly by size and partly by the number of leaves. It is generally possible to see the remains of previous years' leaves at the base of the plant, and these can be grouped into ages by their different stages of decay. Approximate living leaf numbers and their diameters are given:

"0" year, two cotyledons and two leaves, 2·5 mm. diameter.

"1" year, three or four leaves, often smaller than the "0" year leaves, 2·5 mm. diameter.

"2" year, three or four leaves, 2·7 mm. diameter.

"3" year, three or four leaves, 3·4 mm. diameter.

"4" year, and "5" year, the plants vary much in size and may have four to five much larger leaves, 6 mm. diameter.

Saxifraga rivularis *and* Cerastium cerastoides (Pl. VI A)

The age of both these species is difficult to determine as the leaves usually remain green all the winter and there is often considerable individual variation. By grouping the leaves in age groups, starting from the cotyledons, it is generally possible to arrive at an age but this is clearly more liable to error than those discussed previously. Nevertheless, the judgment of the ages of the seedlings in two successive years gave the corresponding age in the great majority of cases.

Salix sp.

The ages were determined by size entirely as most plants produce only two leaves each year until they are 3–5 years old.

Saxifraga nivalis

This species tends to grow very uniformly in the quadrats mapped and the age determination is easy in spite of the fact that two to four leaves grow every year until the plants are 3 or 4 years old. The presence of the dead leaves at the base of the plant, grouped in ages, is a very great help in judging the age, as is also the fact that the plants increased tolerably uniformly in size from year to year.

Saxifraga oppositifolia

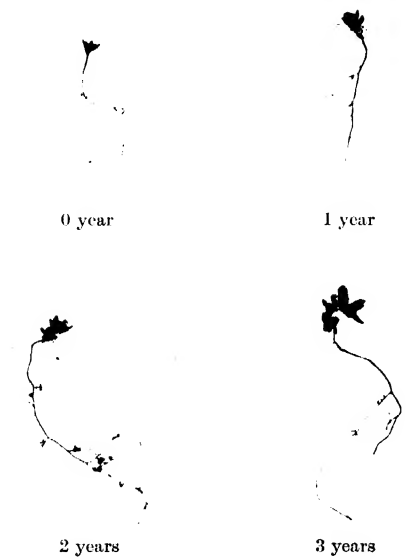
Saxifraga oppositifolia is one of the slowest growing of the species mapped and at the outset it is one of the smallest. The "0" year plants have rather large and fleshy cotyledons with two minute and undeveloped bud-like leaves round the growing apex. "1" year plants grow a pair of leaves and the cotyledons remain functional. The "2" year plants grow a second pair of leaves and in the following year a third pair is grown and the first ones die. By the fourth year a healthy plant has about 3 mm. of bare stem and on top of this 4 mm. of stem clothed with leaves both living and dead. The length of the leaves is about 1 mm.

Location of the quadrats and their soil types

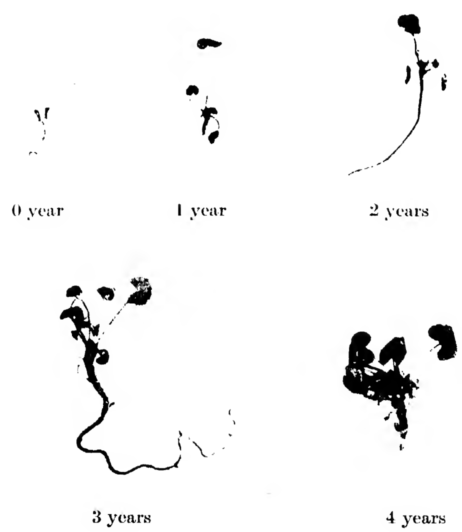
The general aspect of the quadrats and their situation relative to glaciers and snow fields may be seen from the map (Fig. 1). The exact location[1] of the quadrats, marked in the map by lettered dots, was as follows:

1 and 2 were 6 m. above sea-level on the Skaergaards Halvø, Kangerdlugssuak, on an almost level stretch of gabro gravel, *A* on the map.

[1] The quadrats, with the exception of 4 and 5, were marked by small wooden stakes and, as decay is so slow in the Arctic, these should remain in place for many years unless accidentally damaged by bears or falling stones. Quadrats 4 and 5 were marked more permanently by small wooden stakes set in concrete bases, and it should be possible to find them for very many years with the help of an accurate description of their position.



A. *Cerastium cerastoides.*



B. *Oxyria digyna.*

The plants are reproduced natural size.

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3 was 5 m. above sea-level on river gravel on the mainland opposite to quadrats 1 and 2, *B* on the map.

4, 5, 6, 7 and 8 were on a south-east facing moraine of the glacier connecting Mikis fjord and Kangerdlugssuak. 4, 5 and 6, point *C* on the map, were at an altitude of 200 m., 7 and 8, point *D*, were at 130 m.

9 was about 110 m. high on an old and considerably colonized moraine about half way along the north side of Mikis fjord, *E* on the map.

10, 11 and 12 were 110 m. high on the moraine at the end of the valley running northwards from the head of Mikis fjord, *F* on the map.

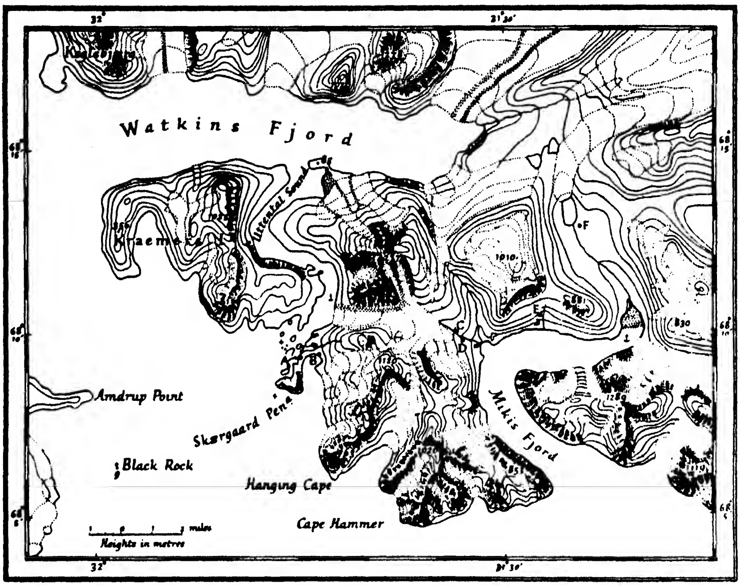

FIG. 1. Map of the South East portion of Kangerdlugssuak and Mikis fjord showing position of quadrats (see text). (Redrawn from maps of the Geodetic Institute, Copenhagen.)

The original intention was to work exclusively on moraines, and eight out of twelve of the quadrats were situated on young moraine, one on old moraine and three on gravel of a non-moraine origin. One of the advantages of investigating moraine areas is that there is presumably a primary colonization taking place, although very slowly. The rocks composing the moraines were either tertiary gabro or else a mixture of this and basalt lava. Both of these are quick weathering and may be expected to produce an adequate supply of nutrient salts. The non-moraine quadrats were on a gravel formed from the break up of the gabro with a considerable admixture of gneiss. The type of result obtained from both the moraine and non-moraine localities was the same.

The object of the mapping, as has been stated previously, was to investigate the survival rate of the seedlings and young plants, and hence areas had to be

selected which contained a large number of young plants. This point is emphasized, as it is not suggested that the density of plants on the quadrats is the average density of the moraine "fjaeldmark". On the other hand, the general conditions of survival are not likely to change with the density of the plants until they can reasonably be said to be contiguous; a condition never reached even on the densest quadrats. The only effect of doing random sampling would have been to have made it necessary to map a much greater area, and the time available was not sufficient. The quadrats were in general selected so as to include an adult plant that appeared to have flowered freely during the last few years, but areas in which the ground was so stony as seriously to restrict seedling growth or so wet as to be liable to solifluxion were avoided. Also, to get good growth of young plants the surface stability had to be suitable; this condition was generally controlled by the inclination of the moraine. The amount of any moraine suitable for study varied greatly, and the differences could generally be associated with the aspect and inclination of the slope. The Lake valley moraine, on which were quadrats 10, 11 and 12, was so uniform over a considerable area that sampling by throwing a stake at random could be adopted, and this was done for quadrats 10 and 11.

The soil types of the quadrats varied greatly and may be grouped as follows. Quadrats 1, 2 and 3 were gravel on the surface and more earthy below with a few large stones embedded in the surface. Quadrats 4, 5, 6, 7, 8, 10 and 11 were on moraine silt with large pebbles and stones embedded in it and with the surface rather firm. Quadrat 9 was on an old moraine and approximated to more normal earth and in late summer its surface was dry and dusty. Quadrat 12 was a fine clayey type of moraine silt, and on it lived the most luxuriant vegetation of the whole of the Lake valley moraine. It tended to have few surface pebbles and was in consequence of its clayey nature rather damp.

The water content of the quadrat soils was not determined, but general observations were taken. Quadrat 9 was the driest both in the autumn and in the summer. All the other quadrats in the autumn were dry on the surface, but at a depth of 1 or 2 in. the soil looked damp. In July and the beginning of August they were damp to within about half an inch of the surface, so it is very improbable that the older plants, at any rate, were short of water.

Finally, it should be said that within a few hundred yards of all the quadrats there were closed associations of plants growing on slopes of the same general aspect.

Results of the mapping—the survival rate

The number of individuals of each species belonging to each age group, recorded in the 1936 mapping of the quadrats, has been counted, and these results are given in Table I. The figure following the number of the quadrat is its area in those cases where this differed from 1 sq. m. In the extreme right-hand column of the table is shown the total numbers of individuals in

each of the quadrats, and along the bottom of the table the total number of plants of all species in each of the groups.

Table I

Quadrat number and area. Plant species	0 yr.	1 yr.	2 yr.	3 yr.	4 yr.	5 yr.	"*a*"	"*A*"	Total
Quadrat 1									
Cerastium cerastoides	10	60	23	9	4	.	3	2	114
Grass and *Salix* sp.	.	2	.	1	.	.	.	.	
Quadrat 2									
Cerastium cerastoides	26	36	19	4	1	1	2	5	100
Oxyria, Salix, Phippsia, Minuartia	.	2	.	1	.	.	3	.	
Quadrat 3									
Oxyria digyna	52	101	43	12	2	.	1	2	520
Cerastium cerastoides	11	4	2	5	2	.	5	5	
Saxifraga nivalis	8	17	6	1	4	.	.	7	
Saxifraga rivularis	59	34	21	40	10	.	32	9	
Minuartia, Carex, etc.	5	4	3	3	1	1	4	4	
Quadrat 4									
Luzula spicata	19	33	30	5	1	1	1	1	92
Salix	.	.	.	.	.	.	1	.	
Quadrat 5									
Trisetum spicatum	11	69	41	7	.	.	.	4	132
Quadrat 6									
Oxyria digyna	4	13	13	4	4	.	.	1	42
Grass	1	2	.	.	.	.	.	.	
Quadrat 7									
Saxifraga nivalis	3	20	18	8	4	.	2	.	316
Trisetum spicatum	8	97	65	25	21	18	11	2	
Salix, Luzula, Oxyria	3	6	3	1	1	.	.	.	
Quadrat 8. 0·5 sq. m.									
Saxifraga oppositifolia	59	98	22	9	3	4	4	1	200
Quadrat 9. 0·4 sq. m.									
Luzula sp.	3	46	11	4	4	3	1	2	117
Cerastium cerastoides	.	4	7	3	.	2	1	1	
Oxyria, Salix, grass, etc.	2	8	10	1	1	1	1	1	
Quadrat 10									
Trisetum spicatum	4	32	14	6	2	.	3	1	139
Oxyria digyna	26	21	.	3	1	.	1	1	
Salix glauca	3	2	6	3	1	2	2	1	
Etc.	.	2	.	2	.	.	.	.	
Quadrat 11									
Trisetum spicatum	2	21	4	1	2	1	1	4	79
Oxyria digyna	.	12	4	5	7	2	.	.	
Salix, Minuartia	.	3	.	5	3	.	1	1	
Quadrat 12. 0·5 sq. m.									
Grass sp.	8	128	70	29	3	3	3	1	359
Oxyria digyna	3	58	26	6	4	7	1	.	
Salix, Cerastium, etc.	2	.	4	.	1	.	2	.	
Total	**332**	**935**	**465**	**203**	**87**	**46**	**86**	**56**	**2210**

The number of seedlings in the age groups from 1 to 5 shows a fairly regular decrease of about 40–60 % each year. As the "*a*" class covers 4–5 years and the "*A*" class an indefinite but large number of years, this decrease must be continued for many years beyond the 4 years shown by the yearly groups (although probably at a slower rate). The "0" year class is a very small one in nearly all cases, and it would appear therefore that the year of the investiga-

tion was a bad one for seedlings for some reason. Exceptions to this are *Oxyria digyna* in quadrat 10 and *Cerastium cerastoides* and *Saxifraga rivularis* in quadrat 3, but even in these instances the "0" year figures are not so high as would be expected from the "1" year figures and the mortality rates for the other years. It might be supposed that the low number of "0" year was due to imperfect mapping, but this is improbable because in 1935 the "0" year class was by far the largest, corresponding to the large "1" year class of 1936, and also *Saxifraga rivularis* and *S. oppositifolia* which are the smallest and most difficult to map both show a relatively large "0" year class. A possible cause of the small number of "0" year plants in 1936 is the fact that the previous autumn was exceptionally dry and snow free, and this may have led to a scatter of the seeds and hence to a reduction in number near to an adult in 1936.

The plant counts for quadrat 4 are given in more detail in Table II (after a few corrections for the age of the seedlings have been applied). This is possible as an almost complete tracing of the individuals from 1935 to 1936 could be carried out because the stiff leaves of the *Luzula* do not die away, so that the plants are almost as easy to see in the autumn as in the summer, and during the 1936 mapping careful search was made for any missing individual. The actual number of dead individuals of each age present on the quadrat in 1936 is given, but this only accounts for about a half of the individuals missing and the rest must have either got buried under the pebbles or blown away. In all forty-six individuals have gone out of a total of 110 in 1935. This agrees well with the death rate deduced from the totals for seedlings of all species on all quadrats.

Table II. *The age distribution of* Luzula *plants found on quadrat* 4 *in* 1935 *and* 1936

	0 yr.	1 yr.	2 yr.	3 yr.	4 yr.	5 yr.	"*a*"	"*A*"
1935 mapping, September	67	41	8	1	1	.	1	1
1936 mapping, July	19	33	30	5	1	1	1	1
Dead with same age as previous year, i.e. died before new growth	10	3	1	.	.	.	.	.
Dead with new age, i.e. died after growth in the spring	7	9	2	2	.	.	.	.
Untraceable, so dead and either blown away or buried	15	6	.	.	.	.	.	.

Totals—1935: 120.
1936: 91. Died 55. New plants 26.

In some of the quadrats many plants were mapped as being unhealthy in appearance, but in others this group was not so noticeable, probably partly due to actual real variation in the quadrats and partly because the condition was much more difficult to observe in some plants than in others. Examples of this were 18 unhealthy plants out of 106 in quadrat 4 in 1935, 12 out of 139 in quadrat 10, and 30 of the 247 grass plants in quadrat 7. It is to be presumed

that most of these unhealthy plants would die before long and their presence is interesting as showing a preliminary stage in the death of the plants. This point will be returned to when discussing the possible causes of the high mortality rate observed in the quadrat plants.

GROWTH RATE OF PLANTS IN THE "FJAELDMARK"

The pressed plants, mentioned previously and used for determination of dimensions and photographing, have been weighed and the weights of some of the series are shown in Table III. The average weight of the plants in an age group is given in black type and under it in ordinary type the weights of the individual members of the group.

The number of plants that were collected in any given age group is too few and the environmental conditions of their growth too varied for the average weights to be more than a rough guide to the growth rate. Nevertheless, these weights are sufficient to show the slow growth rate of the "fjaeldmark" plants, and they also illustrate the rather different growth rates found in different situations as two series of weights are available in several cases, the plants for one series being from a more favourable, and for the other from a less favourable locality.

Considering the table as a whole the most striking point is that the dry weight of the plants increased at most two to three times each year of growth; an amount comparable to the weekly increase in dry weight of an annual plant in temperate regions. There is a considerable scatter of values in each age group, but this is only to be expected, as the plants were collected from among stones and pebbles and no especial care was taken in the collection of the roots, and so the proportion collected in different specimens varies greatly.

A comparison may be made between the weights of the *Cerastium cerastoides* plants collected near to quadrats 1 and 2 (series 1 and 2). These two localities are similar in aspect and situation but differ in that quadrat 1 is kept wet by a small stream during the spring and early summer, whereas from the time of the melting of the snow quadrat 2 dries up progressively as the summer advances. The two series of weights commence at the same value, and by the time the 4th year is reached the quadrat 1 plants are about 2½ times as heavy as those from quadrat 2. This difference in weight but poorly reflects the diversity in size and appearance of the plants. Those from quadrat 1 are large leaved and straggling, whereas those from quadrat 2 are small leaved and very contracted, with the leaves set very close together. The contrast in appearance is such as would be expected from the different water relations of the two habitats.

The *Trisetum* plants of series 7 and the *Luzula* plants of series 5 were collected in a warm valley about 30 m. above sea-level, where some of the earliest vegetation appeared in the spring and where the association was locally closed. These may be compared with series 6 and 4, the plants of which were collected

Table III. *Dry weights of young plants in mg.*

Series	Plant and locality	Date collected	0 yr.	1 yr.	2 yr.	3 yr.	4 yr.	5 yr.
1	*Cerastium cerastoides* Near quadrat 1	15. viii. 36	**0·65** 0·7, 0·6	**2·27** 2·1, 2·0, 3·0, 2·0	**6·3** 7·6, 5·0	**15·5** 15·5	—	—
2	*Cerastium cerastoides* Near quadrat 2	15. viii. 36	**0·6** 0·6	**1·3** 1·1, 2·4, 1·8, 1·1, 1·2, 1·2, 1·3, 1·2	**3·3** 2·1, 3·2, 4·5, 3·5	**6·1** 6·1	—	—
3	*Saxifraga nivalis* Near quadrat 3	14. viii. 36	**0·21** 0·25, 0·15, 0·15	**0·85** 0·8, 0·9	**2·3** 3·4, 2·0, 1·4	**6·2** 6·2	—	—
4	*Luzula spicata* Near quadrat 4	11. ix. 35	**0·45** 0·65, 0·45, 0·45, 0·25	**1·0** 0·9, 0·7, 1·4, 1·1, 0·9	**1·6** 1·6	**2·8** 2·8	—	—
5	*Luzula spicata* Near base	1. vi. 35	**0·34** 0·3, 0·3, 0·25, 0·4, 0·5, 0·3, 0·35, 0·4, 0·3, 0·35	**1·2** 1·1, 1·1, 1·0, 1·5, 1·3, 1·3, 1·0, 1·1	**1·9** 1·9	—	—	—
6	*Trisetum spicatum* Near quadrat 5	15. ix. 35	**0·6** 0·4, 0·4, 1·0	**0·65** 0·7, 0·6	**0·8** 0·8	**2·2** 1·6, 2·4, 2·5	**4·4** 4·4	— —
7	*Trisetum spicatum* Near base	6. vii. 36	**0·4** 0·5, 0·6, 0·3, 0·4, 0·4, 0·25, 0·3, 0·35, 0·3, 0·5, 0·55	**1·2** 1·3, 0·9, 1·6, 1·4, 1·5, 0·7	**1·4** 1·0, 1·3, 1·6, 1·9, 1·6, 1·2, 1·2	**2·6** 2·9, 3·2, 2·8, 1·7	**6·4** 6·4	—
8	*Oxyria digyna* Near quadrat 6	10. vii. 36	**0·4** 0·4, 0·4	**1·2** 0·9, 1·3, 1·3	**2·1** 2·5, 2·0, 1·5, 2·6	**7·3** 6·9, 7·8	**18·2** 17·1, 19·3	—
9	*Saxifraga oppositifolia* Near quadrat 8	10. vii. 36	**0·35** 0·3, 0·4	**0·48** 0·3, 0·5, 0·6, 0·6, 0·4	**0·80** 0·7, 0·6, 0·5, 0·9, 1·0, 0·8, 0·6, 0·8, 1·2	**1·2** 1·5, 1·5, 1·3, 0·7, 1·5, 0·7	—	**2·0** 2·0

near to quadrats 4, 5 and 6. In making the comparison it should be borne in mind that the plants from the moraine (series 6 and 4) were collected in the late autumn and the two other series in the early spring, so that the Nth year of series 7 and 5 corresponds most nearly to the $N+1$th year of series 6 and 4. Making this allowance the series from the warmer locality are in both cases about double the weight of the series from the moraine.

These three pairs of comparable series of weights show the effect of local environment on the growth rate, and suggest that the variation from a closed to an open association is an expression of the different growth rates which are found, as the growth rate probably reacts in some complicated way on the survival rate in the direction that the larger the growth rate the greater the survival rate.

The survival rate in a totally closed association and in a static open association will be the same and for an open association to change to a closed one the difference in survival rate need be very small, much too small to be detected by work of the type described in the present paper.

CLIMATE

In seeking some explanation of the high mortality rate and the slow growth rate which is observed the most obvious possibility for consideration lies in the climate of the district. With this in view the following short statement of the climate of Kangerdlugssuak for 1935–6 has been prepared from the observations collected by the expedition, and it is concerned only with those factors which are most likely to influence the vegetation. (For further accounts of climate see Manley, 1937, 1938.)

The climatic environment of the plant throughout the year may be divided into three parts, the winter when the ground is covered by a more or less thick layer of snow, the summer when the ground is free from snow and the air is relatively warm, and the autumn which may be free from snow and cold.

On 29 August 1932 there was a fall of snow at sea-level in Kangerdlugssuak, but this melted during the course of the next day. It is probable that this was followed by other falls as these were experienced from 5 to 8 September whilst the expedition was at Angmagsalick, 250 miles to the south, and so the ground was probably snow covered for the autumn of 1932. In 1935 conditions were very different, as there was no precipitation from 24 August to 6 October.[1] During this time the temperature fell rapidly, as is shown by the following figures for the weekly average minimum temperatures: 15–21 September, 28·9° F.; 22–28 September, 25·5° F. and 29 September–6 October, 22·0° F. The plants were so quiescent by this time that, so far as could be seen by examination of various specimens, no frost damage resulted. Subsequent to 6 October the ground was always covered by at least a foot of snow, and during the cold period in January and February by 4–5 ft.

[1] Manley (1938) suggests that a snow free and dry autumn is unusual on this part of the coast.

During the winter months the air temperature was fairly low, the average for January being 3·2° F. and for February 4·7° F., but this was of little importance to the plants on account of the snow layer. A thermometer in the snow at about the surface of the ground was read irregularly during the winter; in the beginning of January the temperature shown was 19·6° F. and thereafter it was about 22° F., as there was more snow, and it changed very little day or night until April, when there was a thaw, after which it never fell much below freezing-point again. The temperature recorded by a thermometer 2 ft. deep in the soil fell very slowly and steadily and reached 30·0° F. about the end of March.

In the warmer places and where the snow was relatively thin the ground started to clear in May; by the middle of June most of the ground was clear and by the end of the month there were only a few drifts of snow left. The quadrats were late in clearing; all appeared between 8 and 25 June, but, as late as 3 July, no new growth was to be seen on quadrat 12. Growth of plants does not commence in most places until the snow has gone, as a layer of ice forms on the surface of the ground during the early stages of thawing and remains until the snow layer is quite thin.

Weekly average air temperatures for June, July and until the expedition left in August are given in Table IV, columns 1–3. Meteorological observations were taken at 10 a.m., 4 and 9 p.m., and the average of the temperatures at these times of observation are given in column 3; they are probably a reasonable approximation to the average day temperature. The average minimum temperature in the Stevenson screen rose just above freezing-point between 14 and 20 June, but light ground frosts persisted most nights until the end of the month and on occasional nights early in July.

Weekly precipitation is given in column 4. This is, on the whole, very low, but, except in places with exceptionally good drainage, the soil remained damp.

The average weekly figures for the relative humidity at the times of observation are given in column 7. It is seen that these are similar to the figures obtained in many parts of England. On the other hand, average figures for relative humidity may be of little value as an index of its effect on plants. This tended to be the case in Kangerdlugssuak where the relative humidity was very often 100 %, and, on the other hand, during the katabatic wind storms fell to 30–40 %. Such periods were never sufficiently prolonged to do serious damage to the plants, but they did cause some of the more mesophytic of the plants to become temporarily flaccid.

During the summer there were several wind storms in which forces of 6–8 were recorded. As the plants are mainly low and often protected by rocks, direct damage was rare. These winds were sometimes "föhn" and in any case fairly warm and dry; an example may be quoted of 26 June when the wind force was 5, temperature 52·8° F. and relative humidity was 33 %. On the

Table IV

Date	Average minimum temp. °F.	Average maximum temp. °F.	Average present temp. °F.	Total rain in.	Cloud: Number of observations with $\frac{7}{10}$ or more low stratus (total 21)	Cloud: Number of observations with $\frac{7}{10}$ or more higher thin cloud (total 21)	Average relative humidity, %: 10 h.	16 h.	21 h.	Weekly
31 May–6 June	29·1	40·9	32·9	1·22	19	0	99	97	95	97
7–13 June	31·5	43·8	36·2	0·07	15	0	74	81	91	82
14–20 June	32·1	47·9	39·0	0·49	8	3	79	73	81	77
21–27 June	33·1	52·2	41·8	0·02	6	3	62	67	75	68
28 June–4 July	36·9	51·1	43·6	0·14	8	6	71	70	77	72
5–11 July	No readings taken			0·00	4	—	—	—	—	—
12–18 July	37·3	52·0	45·1	0·00	2	2	77	68	73	72
19–25 July	33·2	47·0	41·2	0·04	6	4	82	80	79	80
26 July–1 Aug.	40·0	51·0	44·9	0·00	10	2	77	75	73	75
2–8 Aug.	35·5	50·4	42·4	0·25	5	3	68	74	87	76
9–15 Aug.	34·6	46·9	40·4	1·64	11	2	71	86	79	79
15–18 Aug.	38·1	51·8	44·3	0·00	0	0	65	81	73	73

other hand, the air was infrequently calm which is of some importance, as air movement tends to prevent the leaf temperature rising very much in the sun.

The noon light value on a clear cloudless day on 12 June was 72 kilolux. This value was obtained by using a calibrated[1] Weston photronic cell and a micro-ammeter made by the Cambridge Instrument Co. It may be compared with the value of 102 kilolux at Plymouth on 21 June 1932 (Atkins & Poole, 1931). Thus carbon assimilation should not be restricted by light value in the Arctic much more than it is in temperate regions, as the light intensity only exerts a marked influence on the rate of assimilation at values far below 72 kilolux.

The effect of cloudiness on plants is complicated, as it affects many different factors such as the light value, air and leaf temperature, humidity, transpiration and rate of assimilation. The relationship between the rate of assimilation and light intensity, with carbon dioxide at approximately the normal air value, has been studied in the case of two plants by Müller (1928) at Disco in West Greenland and by the writer for several others at Kangerdlugssuak. Broadly speaking light is in excess above 15–20 kilolux at temperatures from 0 to 20° C. In Kangerdlugssuak it was found that this light value was not attained, or only just attained, at noon, when there was a layer of low stratus clouds over most of the sky. To give some idea of the decrease in carbohydrate production to be expected from clouding there is given the number of observations per week (total 21) when there was 7/10 or more of the sky covered by low stratus clouds. Every three of these observations would represent about a day when the rate of assimilation would be less than the maximum possible, for most of the day, owing to the low light intensity. In all 26 out of the 63 days shown in the table had this low light intensity, a rather large proportion.

From the above account it appears that in Kangerdlugssuak the plants are protected by snow during the cold winter and early spring, and sometimes also during the autumn month. Not till late spring when the day temperature is already high and the night minimum is fairly high do the plants emerge, and during the summer there would appear to be no specifically harmful factor at work. It may be concluded that there is no time of the year when the conditions are so unfavourable as to cause serious direct damage to the plants.

Discussion of factors limiting the growth of plants in "fjaeldmark"

The "fjaeldmark" association has been shown to be characterized by a high death rate of an initially large population, the individuals of which have an exceedingly slow growth rate. Many of the young plants were described on the quadrat sheets as being small for their age and unhealthy in appearance (see p. 398). This fact, coupled with the high death rate, suggests that these young

[1] The writer is greatly indebted to Dr H. H. Poole of the Royal Dublin Society for help in the preparation of the apparatus for the determination of the light values.

plants are "weak"; this is a vague term with no definite physiological meaning but it may be used to draw a distinction between a weak plant that dies and a strong plant that is killed by some outstanding external factor, probably of a climatic nature. Such a factor does not appear to exist and it may be concluded that the death of the young "fjaeldmark" plants is caused by some slow acting, and probably internal cause, or set of causes.

Warming (1909) associated the development of "fjaeldmark" with low temperature during the summer months, and this is believed by the writer to be the main factor concerned and will be discussed at length later. Before doing this, various other possibilities and suggestions will be considered. Ostenfeld (1923) comments on the slow growth and longevity of arctic plants and associates their slow development with the shortness of the vegetative period. In the writer's opinion this is only one of the factors responsible for the slow growth.

"Fjaeldmark" has been associated with an unstable soil surface, amongst other things, by Summerhayes & Elton (1923, 1928) when considering Spitzbergen vegetation types. This is certainly not the cause in most of the Kangerdlugssuak area and in particular where the quadrats are situated, as it could easily be recognized by seeing plants being overrun by stones and earth, yet on the quadrats even the minute seedlings were growing upright and undisturbed.

Severe nitrogen shortage has been proposed as the factor restricting the growth of plants in open associations. The nitrogen supply of virgin soil comes from three sources: in rain from the air, nitrification bacteria in the soil and from animal remains and excreta. In the Kangerdlugssuak area the last source of nitrogen is very small, as the only carnivors, the bear and the fox, are rare, as are also sea gulls. The other birds are vegetable feeders and so do not affect the total supply of nitrogen. No determinations of atmospheric nitrogen have been made in Greenland, so the supply from this source can only be guessed at. Russell & Richards (1919) analysed rain water from Iceland and calculated that the nitrogen falling in the rain would be equal to about 1·06 lb. per acre per year. The quantity falling in Greenland would probably be less than this, so the supply of nitrogen from this source is small but quite important acting over long periods of time.

The size of the remaining source of combined nitrogen, the nitrifying bacteria of the soil (no leguminous plants are native of Greenland) is also very difficult to assess. Koch (1907) showed that *Azotobacter* has a marked temperature coefficient for fixation of atmospheric nitrogen and that it ceases measureable activity at about freezing-point. Thus it would be expected that most nitrification would take place in the warmer places, where in fact most plants grow.

On the other hand, there are facts which suggest that lack of combined nitrogen is not the controlling factor in the formation of "fjaeldmark". First, the adults are large and healthy and not noticeably smaller than the plants of

the same species growing in the neighbouring closed associations or in Iceland or in Great Britain. Secondly, if it were supposed that an adult accumulated a supply of combined nitrogen over a long period of years it would be expected that when it died other plants would grow in the same place, utilizing the combined nitrogen which was being slowly produced by its decay, and such plants should be larger and more healthy than others growing a small distance away. Such a process would be expected to produce tufts of vegetation. Neither of these effects were observed, although they were both sought for. Thirdly, nitrogen shortage should operate most severely on adults and least on young plants which start with a supply of combined nitrogen in the seed, whereas the contrary effect was observed.

On the other hand, it must be admitted that an increased supply of nitrogen to arctic plants does cause a more luxuriant growth in the course of time; but the same effect is observed in temperate regions. Further, Summerhayes & Elton (1928) state that in Spitzbergen this nitrophilous vegetation is not a mere development of the normal "fjaeldmark" plants but is a special group of a more sub-arctic type of plant, and it is to be presumed that such plants can grow more strongly in favourable localities than the arctic types. Heavy manuring of the type that produces the nitrophilous vegetation will affect other factors besides the nitrogen content of the soil, such as the water content, and these other factors may be partly responsible for producing the nitrophilous vegetation.

Summing up it may be said that in the opinion of the writer nitrogen shortage is probably one of the factors contributing to the slow growth rate of the "fjaeldmark" plants, but it is believed not to be of major importance.

Shortage of mineral salts is unlikely to occur in the moraine areas worked on, as their soils are the product of disintegration of recent basic igneous rocks which are fairly rich in the required mineral constituents.

Finally, it has been suggested that shortage of water is the controlling factor in the development of plant communities in the Arctic, and for the Kangerdlugssuak area, Bøker (1933) has stressed this view. It is clear that this is true of certain types of locality, such as where there is only coarse gravel or scree, and here in general no plants grow and such places have been excluded from the term "fjaeldmark" as used in this paper. On the other hand, the soil of the "fjaeldmark" usually contains a fair proportion of finely powdered material or silt in the earth, and the water-holding power is, in consequence, considerable, and so water shortage is not a factor greatly restricting plant growth.

It is worth while describing the situations where a luxuriant growth of vegetation develops and contrasting these with where "fjaeldmark" develops. For good growth a sheltered place with a southern aspect is required. The shelter may be supplied by either a small object like a boulder or else a gully or even by the shelter of a hillside. If such a locality is well watered the

climax type of the vegetation of the district develops. On the other hand, places with a good aspect and no obvious water supply have a good growth, as the water in the soil seems to be sufficient to last the short summer. Finally, the time of melting of the snow is very important and is closely correlated with the summer temperature. In fact a warm place generally has a long period of summer conditions. On the other hand, "fjaeldmark" develops in unsheltered places which are also damp and are often, as in the moraines investigated, subject to small local cold katabatic winds from some glacier or snow field above them. These winds seem to blow almost continuously in the summer and tend to keep the temperature both of the soil and of the leaves of the plant lower than that of sheltered situations or of localities which are not below glaciers or snow fields.

The above discussion may be summarized by saying that in the writer's opinion restriction of growth in the "fjaeldmark" areas under consideration is chiefly controlled by internal growth factors and not by the supply of salts, water or combined nitrogen, although the possibility of shortage of nitrogen is stressed as being possibly a contributory cause. In considering the possible internal factors the writer has come to the conclusion that the "weakness" of "fjaeldmark" plants is due to carbohydrate shortage brought about by the climate of the district. Reasons for this belief will now be given.

The growing period of these arctic plants lasts for only six to nine weeks. Such a length of time is adequate for growth and reproduction in temperate or tropical countries (cf. the ephemerals) but on account of the low temperature it is apparently barely sufficient for life in the Arctic. It may be pointed out that the "fjaeldmark" clears of snow in the spring three or even four weeks later than the nearby closed associations.

Temperature, the most important factor in the environment, is very complicated in its effect as all phases of the plant's metabolism are influenced. The direct effect on the growth rate is believed to be of small importance in the Arctic because the leaves are few in number and are produced rapidly in the spring weeks, and thereafter increase in size of the plant ceases for the year. Thus the situation is essentially different from that of a temperate locality where the curve of growth shows the approximately exponential form even in a single season and in such a case alteration in the growth rate (i.e. rate of cell division and cell increase in size) would be of great importance each season. The arctic herbaceous plants correspond in this respect much more to the tree type of growth where a burst of leaf production takes place in the spring and then the tree spends the rest of the summer accumulating food reserves for the following year's growth. The actual rate of assimilation of arctic plants lies in the same range of values as that of the temperate plants (Müller, and determinations by the writer).

Studies carried out in temperate regions have shown that temperature exerts a marked influence on the "unit leaf rate" and on the "nett assimilation

rate" (cf. Briggs *et al.* 1920; Gregory, 1926). Since the "unit leaf rate" is presumably controlled partly by the "nett assimilation rate" and partly by the rate of growth both these results show that temperature strongly influences the rate of accumulation of carbohydrate in a temperate climate. This effect which occurs where the air temperature lies between 12 and 20° C. would be expected to be greater in the Arctic where the range is 3–8° C.

Further the total carbohydrate production of the Kangerdlugssuak plants here considered must be considerably reduced by the number of heavily overcast days. Nearly one-third of the summer was so dull that the rate of assimilation of the plants was "light limited" except for a short period about noon (see p. 404). In effect, this means that the summer, so far as carbohydrate production is concerned, is shortened by about one-third.

It may therefore be concluded that any plant growing in the Arctic is near to its subsistence level for carbohydrate production, yet the adults appear to be healthy and to live for long periods, whilst about one-half of the young plants die each year. The following suggestions are put forward in an attempt to explain why this factor should operate more severely in the case of young plants than old.

(1) Adults require an excess of carbohydrate for the production of seeds only, whereas young plants require an excess so that they can double to treble their dry weight each year. Further this has to be entirely produced by an unchanging area of leaf, not as in a herbaceous plant growing in temperate regions where the leaf area increases continuously with dry weight. It is possible that if the young plants cannot increase at this rate, i.e. two to three times each year, they will slowly die.

(2) It has been shown that the ratio of leaf area to dry weight is low for young plants (cf. Briggs *et al.* (1920) working on Kreusler's data for *Zea*, and Brenchley & Jackson (1921) working on barley) and that the ratio of root to top of a plant is high (cf. Brenchley (1920) working on barley). Thus for a given leaf area respiration losses are greater for young plants than for old and non-reproductive expenditure of carbohydrate is also greater.

(3) If one of the leaves of a young plant gets damaged, due to frost or some other cause, the loss of leaf area would probably be sufficient to cause the death of the plant, as one-half to a third of the leaf area would be destroyed. Partially damaged leaves were observed in the spring, especially the ends of the grass and *Luzula* leaves. This slight frost damage would have relatively much less effect on an adult plant.

(4) Any slight water shortage which there may be will be much more serious for small plants with a root system penetrating at the most about two inches into the soil, as it is this upper layer that will tend to dry up while the deeper layers will remain damp. Overheating by the sun may also be significant. Both these factors may tend to cause a closing of the stomata and so a reduction in the amount of carbon assimilated. The resultant difference in the growth rate

is clearly brought out by a comparison of the dry weights of the *Cerastium cerastoides* plants collected adjacent to quadrats 1 and 2. The actual difference in dry weight for the three-year-old plants is from 15·5 mg. on quadrat 1 to 6·1 mg. on quadrat 2.

(5) Young arctic plants never produce more than one set of leaves in a year. Presumably this is because it is not economic to produce a second crop as they would have such a short functional period as even to fail to make good the expenditure of carbohydrate on them. This is no drawback to a plant in a more or less static condition but it means that the growth will be very slow.

The above is only a short discussion of the subject and is put forward to give general support to the suggestion that these arctic "fjaeldmark" plants during their phase of active growth are restricted by a carbohydrate shortage. It is obvious that much experimental work would have to be carried out on the growth rate, respiration rate, and "nett assimilation rate" in the Arctic before the suggestion made could be regarded as more than a tentative explanation.

Viewing the life of these plants a little more broadly, it seems probable that the survival rate is as low as is compatible with the survival of the species in the area and this probably means that the growth rate is about as low as is compatible with the individual plant's survival. It is unusual to have an association which is apparently stable and which depends on the maintenance of an unchanging average survival rate over long periods of time. Probably this is made easier by the fact that the adults live for a long time, 30–40 years in many species, and so small variations in the survival rate, over periods of even 10–15 years, will not seriously affect the association. Such a situation is essentially different from that found in a closed association where the death rate of a species is controlled by the intensity of ecological competition.

SUMMARY

A study of plants growing in "fjaeldmark" of the Kangerdlugssuak area of East Greenland was undertaken during 1935–6.

Twelve quadrats were laid out and mapped and each plant was recorded with its age. From these maps it is shown that about 50 % of the plants under the age of five years die each year and it is inferred that this rate of death continues for probably another equal period.

Plants from the "fjaeldmark" were collected, pressed, and have been weighed. It is found that there is only a two- to threefold increase in dry weight each year.

An account of the climate of the district is given.

In the discussion of these results it is suggested that the primary cause of the slow growth rate and high death rate is that young arctic plants are suffering from a carbohydrate shortage and reasons in support of this are given. The importance of nitrogen shortage is considered in detail and it is concluded that this is not of primary importance.

The field work of this investigation was carried out jointly with my wife, who has also given me much help in numerous discussions during the working up of the results. I should also like to thank my brother, L. R. Wager, for discussing problems of arctic vegetation with me on many occasions and for correcting the manuscript.

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EDAPHIC FACTORS IN THE DISTRIBUTION OF AQUATIC PLANTS IN THE ENGLISH LAKES

By R. D. MISRA

(*With six Figures in the Text*)

The distribution of aquatic plants in nature has been found by most recent workers, notably Brown (1911, 1913), Pond (1905) and Pearsall (1920, 1929), to be related to the nature of the substratum. This fact is rather opposed to the general belief that the submerged aquatic plants derive their nourishment from the surrounding water and the substratum provides only a medium for mechanical support of the plants (cf. Welch, 1935).

The present study aims at a close investigation of the relation of the aquatic plants with the chemical and physical nature of the substratum in the English lakes. Although it deals only with edaphic factors, actually the whole question of the habitat factors concerned in the distribution of submerged aquatic plants in these lakes has been reinvestigated. It was found, in agreement with Pearsall (1920), that it was impossible to correlate this distribution with differences in the waters such as those of temperature, of gas content or of other dissolved substances like ammonia—known to show some variation. The results are given elsewhere (Misra, 1937) and filed for reference at the Wray Castle Laboratory.

Thus it certainly appears that the distribution of aquatic plants is controlled by the chemical and physical properties of the lake shore, and accordingly, while a preliminary survey of the possible edaphic factors was in progress, an attempt was made experimentally to show the dependence of the plants on the substratum. Two sets of culture experiments were done—one in Lake Windermere and the other in the laboratory.

Experiment A. In Lake Windermere

Six similar *Potamogeton perfoliatus* seedlings were obtained from the same place (growing in Fisherty How Bay) and were transplanted in glass jars each of which contained the same quantity of three types of muds collected from different localities in the lake. Each of these contained two seedlings of the plant. These jars were sunk in a small bay of the lake at a depth of 1·5 m. to obtain normal and identical environmental conditions except for the nature of the mud. Mud I was from below *Isoetes*, mud II bore *Potamogeton perfoliatus* in nature and mud III had a natural vegetation of *Sparganium minimum* and *Potamogeton alpinus*.[1] The plants were allowed to grow in these jars for a

[1] The plant names used are those of Stapf (1929).

month and then harvested. The amount of growth as obtained by weighing the plants in each case is expressed below (Table I).

Table I

Jars	Mud type	Humus % dry wt.	Crop weight in g. Fresh wt.	Crop weight in g. Dry wt.
I	Inorganic coarse brown silt	8·04	3·75	0·467
II	Moderately organic black flocculent mud	12·26	8·62	0·778
III	Highly organic brown mud	24·00	3·05	0·298

Thus the best growth of *P. perfoliatus* has been obtained in jar II and the poorest in III. This is in conformity with the natural distribution of the plant.

Experiment B. In laboratory

The same three types of muds as used in the lake culture experiment were allowed to stand with distilled water in glass jars for about six months. This time a number of seedlings of *Potamogeton perfoliatus*, *P. alpinus* and *Sparganium minimum*, obtained from Lake Windermere, were planted in the jars which were then placed under identical conditions of light and temperature. The water in the jars was aerated from time to time. Table II shows the observations made.

Table II

Jars	*P. perfoliatus*	*P. alpinus*	*Sparganium minimum*
I	Grew well for 20 days and then died	Grew well but narrower and greener leaves produced than found in the lake	Slow growth
II	Perfect growth until the end of the exp.	Poor growth but survived till the end of the exp.	Growth poor
III	Died within a week	Grew well with normal type of leaves	Grew vigorously, many plants came out of the rhizomes
Duration of exps.	4. iv. 35 to 24. v. 35	24. iv. 35 to 24. v. 35	12. v. 35 to 24. v. 35

Owing to the death of some of the plants, weights were not taken. But the above observations are again in conformity with the natural distribution of the species studied except that *P. alpinus* does not occur in the lake on type I mud even in the form which grew in that jar. The fact that *P. alpinus* could grow on this mud suggests that these coarse inorganic silts are in some respects ecologically similar to the peaty muds. This is borne out by analyses given later as well as by other facts. Thus *Juncus fluitans*, a plant commonly found on highly organic muds, may also occur on coarse inorganic sediments at times (see Pearsall, 1920).

Thus it will be seen from the evidence presented by the above tables that edaphic factors are very important in influencing the development of vegetation in the English lakes. Hence a detailed study of lake muds in relation to plants and plant communities has been undertaken.

1. PHYSICAL CHARACTERS OF SUBSTRATA

The English lakes were formed by glacial action which dug out their basins. The underlying rocks are essentially similar, consisting of slates, grit and flags of Silurian age. But although the lakes are of the same age and origin yet they have developed into very diverse forms. This diversity is mainly due to two factors, the varying hardness of the underlying rocks and the varying intensities of the factors causing erosion and deposition.

Pearsall (1920, 1929) has shown that the moulding of shores depends upon the intensity of wave action and the nature of the marginal rocks, whether hard or soft. The prevailing winds cause the rising of waves which become bigger in proportion to the distance they travel. These waves break down the shore line by erosion and redistribute the material in the littoral region. Eventually a wave-cut terrace is formed of gravel with a steep slope of sand. Silt and finer sediments tend to be deposited in deeper water. In these lakes such wave-cut terraces are quite common and they are usually colonized by *Littorella uniflora*. This plant grows in swards and binds the loose sand and gravel of the shore. In deeper waters just below the terrace where sand and silt have been deposited *Isoetes lacustris* finds its place, and generally below this plant there is likely to be a zone characterized by finer and deeper silt with *Nitella opaca* or *Potamogeton perfoliatus* which have replaced the first colonist, *Isoetes*. This process of silt and vegetational zonation depends upon the locality and the rate of silting. Thus, sheltered places tend to become colonized early and their vegetation and muds may have progressed a long way from the starting points. Pearsall shows that two factors may affect the rate and direction of the progression—the rate of silting, bringing in inorganic matter (and probably bases, e.g. potash in Pearsall's results), and the resultant rate of accumulation of organic matter. But in a lake like Windermere the *normal* plant succession is clear. In deeper water (e.g. 2-6 m.) *Isoetes* (I) is followed by a group of species (II) *Potamogeton perfoliatus*, *P. praelongus*, *P. lacustris* and *Nitella opaca* (with a much wider range). Then thirdly (III) come *Sparganium minimum*, *Potamogeton alpinus* and *Elodea canadensis*. At this stage the vegetation is often sparse and often extensive bare areas occur, called in the subsequent text *sterile* muds. Then finally, water lilies and reeds usually develop. The main part of the work described here is concerned with the description of the properties of the soils characteristic of these main stages. This is partly because this succession is the main feature of the northern part of Windermere as well as of other lakes (see Pearsall, 1920), but also because both vegetation and the silts in deeper water (2–6 m.) show less variability from the typical succession. The complexity of the possible successions is shown in Pearsall's papers.

2. Organic matter and plant successions

The development of the plant successions is usually marked by increasing organic content of the substratum (data in Appendix II). It will be seen that the early colonizers, viz. *Littorella* and *Isoetes*, are most common up to 10 % of organic matter in a dried sample of the mud. *Potamogeton perfoliatus*, *P. lacustris* and *P. praelongus* on the other hand occur most frequently on substrata containing between 10 and 20 % of organic content. When the substratum becomes still more organic *Sparganium minimum* and *Potamogeton alpinus* grow there better than other submerged species. *Elodea*, *Potamogeton obtusifolius* and species of *P. natans* also occur on such soils. *Carex* (*C. vesicaria* and *C. inflata*) can grow upon substrata containing more than 40 % of organic matter.

Thus it will be seen that the plant successions and the organic content of the substratum run broadly parallel to each other. However, some disturbance of an exact sequence may be caused by abundant silting in certain localities. As a result of this silting the earlier members of the succession seem to persist for a longer time on more organic soils than is really usual in undisturbed areas. For instance, *Littorella* in association with *Phragmites* in shallow water and *Potamogeton perfoliatus*, *P. praelongus* and *Isoetes* in deeper water are locally frequent in Congo Bay upon muds containing more organic matter (+24 %) than is usual for these species (nos. 25, 28–32). This unexpected distribution of the species is correlated with the presence of abundant silt brought down by the Blelham Beck. A similar type of habitat seems to be responsible for local growths of *Littorella* associated with reeds in Pullwyke Bay (no. 6).

Sources of organic matter deposited upon the lake bottom

There are chiefly two possible sources of organic matter present in the bottom deposits of a lake. Swedish limnologists have called these "allochthonous" when the organic matter is derived from external sources and "autochthonous" when it is developed from the lake.

(*a*) *Derived from external sources.*

In many lakes a large proportion of organic matter is derived from terrestrial vegetation. A lake with well-timbered shores will accumulate large quantities of air-transported leaves during the autumn. Moreover streams, especially when in flood, wash down twigs of trees and other dead vegetable matter into the lakes. There is usually a well-defined zone of dead leaves and twigs outside a stream mouth (cf. Pearsall, 1920).

(*b*) *Developed within the lake*

The littoral flora and fauna together with the plankton of a lake contribute to a varying extent to the bottom deposits. In the former case the area of littoral region in proportion to size of the lake is an important factor as also

are the areas of sheltered and abundantly silted regions in the lake. This is because the rooted vegetation can develop luxuriantly near such places. With the exception of Wastwater and Ennerdale, all the other English lakes possess large shallow tracts where rooted plants can grow. Another source of organic matter is the plankton. The plankton of Lake Mendota, according to Birge & Juday (1922), can produce about 12,000 kg. of dry organic matter per hectare of surface area. No such estimates are available as yet for the English lakes, but the amounts of plankton are probably much smaller.

(c) *Chemical nature of the organic matter*

The organic matter derived from external and internal sources tend to be mixed up and distributed more or less equally on the lake floor. At present there is no method of deducing how the proportions of organic matter derived from the two sources vary in a given mud sample. But the predominance of one type or the other in the local deposits might be rather important in virtue of their different chemical properties.

According to Russell (1932) and Lundegardh (1931) the average C/N ratio for vegetable residues (terrestrial plants) is usually about 40, but it is about 25 for leguminous plants. On the other hand, the aquatic plants have much lower values for C/N ratio than the land plants. Table III, in which the C/N data obtained for some of the plants growing abundantly in the English lakes are given, bears out this fact. Details are given in Appendix VI.

Table III

Species	C/N ratio
Potamogeton perfoliatus	5·50
Elodea canadensis	5·13
Myriophyllum spicatum	6·58
Isoetes lacustris	15·10
Littorella uniflora	15·30
Nitella opaca	5·40
Chara fragilis	5·00
Plankton	*ca.* 6*

* As calculated from Birge & Juday's (1922) figures.

The C/N values for rhizomes and shoots of reeds and sedges vary between about 40 and 90 (cf. Appendix VI), thus these resemble land plants in having a high proportion of carbon to nitrogen.

According to Russell (1932) the organic matter in the soil is essentially a transient constituent. While older material is being continuously decomposed new supplies are being continuously added to the soil. But as Russell says the various decomposition processes in the soil settle down to some kind of equilibrium so that the organic matter remains fairly constant both in amount and in composition. Thus he shows that the C/N ratio of most cultivated soils settles down to about 10–12. In fact he has shown that crops and manures have no influence upon this ratio as obtained for some of the English soils he

examined. This ratio has also been shown to be independent of the organic content of the soils. Thus it will be of interest to know the ratio of carbon to nitrogen in case of submerged muds.

The amounts of humus and nitrogen and C/N ratios are given in Table IV for mud samples obtained from different lakes at great depths. At such depths the organic content of the mud shows little variability. Although the samples have not been obtained from the deepest part of the lakes yet they represent fairly well the conditions obtainable in the profundal regions of the lakes.

Table IV

Lake	Depth in m.	Humus % of dry weight	Nitrogen % of dry weight	C/N ratio
Ullswater	17	10·56	0·2989	17·60
Ennerdale	10	10·76	0·3703	14·50
Ennerdale	50	12·84	0·4506	14·30
Windermere	50	16·84	0·5584	15·10
Coniston	8	18·08	0·6400	14·15
Esthwaite	12	21·34	0·8539	12·50
Blelham Tarn	9·5	24·00	1·0280	11·68

The humus and nitrogen data given in the above table show that with an increase in organic matter the C/N ratio decreases in the mud, that is nitrogen is accumulated more than carbon.

A large number of C/N data obtained for samples of mud collected from different lakes are plotted together against their organic content in Fig. 1. The dominant species growing upon these samples are also indicated on the graph.

In considering the comparative losses of carbon and nitrogen during the decomposition of organic matter in muds reference is made to Fig. 1 again. In general it would seem that the higher C/N values obtained for the comparatively inorganic and peaty muds might be due to plant residues which also have a high C/N ratio. In this case carbon and nitrogen might be lost in more or less similar proportions during their decay. Similarly, the lower C/N values might be due to plant residues richer in nitrogen. But the average C/N ratios of the plants seem to be far away from those for the muds upon which the plants grew. For instance, *Littorella* and *Isoetes* have been shown to possess a C/N ratio of about 15, whereas that of the mud may be higher than this figure. The reeds and sedges on the other hand have C/N values ranging from 40 to 90 both for their shoot and rhizome, whereas the substratum upon which they grow does not usually show a C/N ratio above 30. Again, the pond weeds have much lower C/N values than those of their substrata.

It may be quite possible that the C/N values of the muds discussed above might represent a mean of the values for organic matter derived from external sources and for that developed within the lake. But it is hard to see on this assumption how Ennerdale Lake with rocky and barren surroundings could have a C/N value of about 14 while incoming organic matter from external

sources must be far less than that in other lakes with a more luxuriant terrestrial vegetation surrounding them. Hence it seems that a large proportion of the organic matter must be derived from the plankton and aquatic plants which possess very low C/N values. The high C/N ratio obtained for Ennerdale can only be explained if there are comparatively larger losses of nitrogen than of carbon. On the other hand much bigger losses of carbon than nitrogen seem to be the possibility in case of comparatively inorganic substrata which consist of fine silt and have a very low C/N. These fall below the general curve shown in Fig. 1.

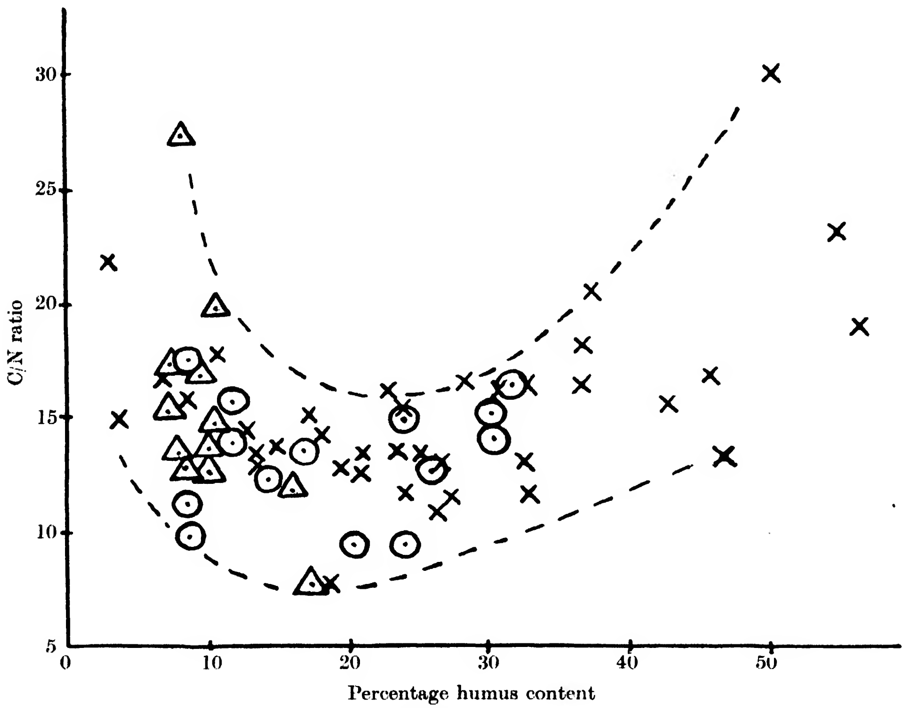

FIG. 1. C/N ratio of muds in relation to their organic content; triangles for *Littorella-Isoetes*; circles for *Potamogeton perfoliatus* with *P. praelongus*; crosses other species or places.

It would appear that with increasing amount of humus in the substratum carbon losses (in comparison to those of nitrogen) increase provided the chemical nature of the original organic matter in all the lakes is very similar. In eutrophic lakes like Esthwaite and Blelham Tarn plankton would be more abundant than in the other lakes. But both of these lakes are also surrounded by large areas of reed-swamp and well-timbered shores. Thus the proportion of organic matter received by these lakes from external and internal sources may not be very different from that obtainable in the other lakes.

The above considerations, therefore, suggest that the C/N ratio of the mud

does not depend to any large extent upon the original chemical nature of the organic matter it receives. This conclusion agrees with the observations of Russell (1932) for arable soils. But in case of the deeper lake muds the gradual decline of C/N ratios is very suggestive of the fact that comparative losses of nitrogen decrease as the organic matter of the sample increases up to 25 %. At the same time the texture of the mud also changes as it becomes finer and more liquid with more organic matter.

It will be subsequently shown that the nitrogen of the organic matter is transformed into ammonia during its decomposition. It seems therefore very probable that, owing to the adsorptive properties of the mud colloids, a large part of the ammonia formed is retained by the mud when it becomes finer. Subrahmanyan's (1927) work also suggests the same fact since he does not find any significant loss of nitrogen from waterlogged soils, although carbon is lost all the time. Fowler's (1934) statements also seem to support this view. According to him there is no loss of nitrogen from paddy fields in India. Further, he states that muds of rivers and estuaries in Germany contain 2–4 % nitrogen, a very high proportion, while in China mud is dredged out and used as a constituent of compost because of its high nitrogen content.

The data of Alexander *et al.* (1935) show no such decline of C/N ratio with increase in organic matter of the muds. The average figure for C/N, as can be approximately calculated from their figures for total nitrogen and percentage loss on ignition, remains about 25 for about 3 to 25 % humus content of the samples. However, they have been dealing with highly polluted areas covered with brackish water in which special types of industrial organic matter and presumably large amounts of acids are discharged from a manufacturing town. Hence their results may not be comparable with those for lake muds. But Boysen Jensen (1914) states that the average C/N for sea muds is about 11·1, whereas it is about 12·5 for sand obtained from the North Sea. Allegeir *et al.* (1932) give a general average figure of C/N for lake organic matter as about 10. Unfortunately, large numbers of such data as obtained for the English lakes do not appear to exist in other countries.

Considering the distribution of species with regard to C/N data, a definite association of the plant successions and the C/N ratio in relation to the humus content of the substratum is suggested in Fig. 1. It is seen from this that as the primitive substratum becomes older by accumulating organic matter, its C/N ratio falls and *Littorella* and *Isoetes* give place to *Potamogeton perfoliatus*, *P. lacustris* and *P. praelongus*. However, as the substratum tends to accumulate peat and consequently raise its C/N ratio *Sparganium minimum* and *Potamogeton alpinus* displace the pond weeds. With a further increase in peatiness and C/N ratio reeds and sedges appear in shallow water and in many cases the mud may become sterile in deeper water. Thus there is found to be a broad parallelism between the plant successions and the development of lake substrata with regard to C/N ratio and organic matter.

3. Hydrogen-ion concentration of typical muds

The increase in organic matter of the muds is not marked by any great change in their acidity. Data for the *p*H values of over 90 muds are given in Appendix II. These show that in general the plants of inorganic soils (the colonists) occur on substrata with a wide *p*H range, 5·4–8·0. As the soil becomes more organic the *p*H range narrows—until finally in the most peaty and organic soils it is between *p*H 5·3 and 5·9 (data for *Carex inflata* and *vesicaria*). The stages in this development are shown in Table V. Numerous figures are available for the first-mentioned plant in each group. The records for the additional species given lie with the *p*H range given and at least suggest a similar range.

Table V

Stage	Species	*p*H range
1	*Littorella uniflora*, *Lobelia dortmanna*	5·5–8·0
	Isoetes lacustris	6·0–7·9
2	*Potamogeton perfoliatus*, *P. praelongus*, *P. lacustris*, *Nitella opaca*	5·5–7·2
3	*Sparganium minimum*, *P. alpinus*, *Elodea canadensis*	5·4–6·5
4	Water-lilies	5·3–6·2
	Phragmites communis	5·3–7·3
	Carex spp.	5·3–5·9

It will be noted that the records for *Phragmites*—a plant which may occur on quite inorganic substrata—also show a wide *p*H range, in contrast to those for *Carices*.

It is evident, however, that the *p*H of the substratum can have little effect on the distribution of the plants because all the species occur in a similar range. On the other hand, the *p*H data do suggest that the influence of the organic matter becomes increasingly dominant as the mud succession develops.

Further, the absence of any very acid soils is remarkable in view of the fact demonstrated later that some of these soils are extremely "unsaturated" with bases or, to put it in another way, very deficient in lime. The low acidity appears, in fact, to be associated with the special methods of decay prevailing under conditions of complete waterlogging, and if muds of this type are allowed to stand in air so that much of the water drains away, their *p*H value rapidly falls. This is well shown in some *p*H data for organic muds from Blelham Tarn given in Table VI.

It, therefore, appears that air is necessary for the production of acidity in these muds, and that the high *p*H values of the native muds are due to the anaerobic conditions under which they exist.

Table VI. *pH values at different times after collection*

Mud no.	Organic content	Days after collection 0	7	12	27
56	46·92	7·08	5·81	5·19	3·90
91	24·00	6·36	4·87	4·92	4·49
92	66·00	5·95	5·06	4·60	4·72
95	31·72	6·58	4·30	4·07	4·13

4. Anaerobic decomposition of organic matter in submerged muds

Absence of oxygen in waterlogged soils is commonly assumed. In these muds it is shown by a variety of facts. Firstly, in the absence of oxygen, sulphur compounds are liberated as sulphides, in aerobic soils they are oxidized to sulphates. Incidentally, Rost (1922) states that the sulphuric acid produced in this way in peaty soils causes a considerable increase of acidity. Secondly, decomposition of nitrogen compounds stops at the ammonia stage and no nitrates are produced. Thirdly, carbon is reduced to marsh gas (CH_4).

According to Allegeir *et al.* (1932) about 65–85% of the gas produced during anaerobic decomposition of bottom deposits obtained from Lake Mendota was marsh gas. At many places in Lake Windermere where the muds are highly organic a large amount of gas is liberated if the peat is disturbed. The gas, when lighted, burns with a flame on the surface of the water and hence seems to be marsh gas. The production of marsh gas is usually more abundant at places where there is rapid silting, indicating a higher rate of decomposition of organic matter.

Presence of sulphides in the substratum

The presence of sulphides in lake muds would indicate the anaerobic conditions prevailing at the lake bottom. Hence a number of typical samples were qualitatively tested for sulphides with filter paper moistened with a saturated solution of lead acetate. The results are tabulated in Table VII.

From this table it appears that, with the exception of the first two cases with low organic matter, all the samples tested show presence of sulphides. However, there does not seem to be any exact correlation between the organic content and sulphide content of the samples studied. Nor do the sulphides seem to be responsible for changes in the type of vegetation.

Sulphides may not be directly harmful to plant growth in the lake unless they produce sulphuretted hydrogen. In an experiment in which mud and water were sealed up for many weeks (see p. 422) no sulphuretted hydrogen could be detected in the water of any of the flasks. The smell of sulphuretted hydrogen was noted only at one place, viz. Congo Bay. The mud here was covered with a thick net of *Chara fragilis*. But it is now doubtful whether the smell was that of hydrogen sulphide, since Haas (1935) has lately shown that a

Table VII

No.	Locality	Depth in m.	Colour	Vegetation	Organic content % of dry wt.	Sulphide content
1	White Cross Bay	1·5	Brown	*Phragmites*	3·90	—
2	Congo Bay	0·8	Red-brown	*Phragmites, Littorella*	5·76	—
3	Fisherty How Bay	3·0	Dark brown	*Isoetes, Littorella*	5·76	1
4	White Cross Bay	1·5	Black	*Polygonium amphibium*	8·66	4
5	Ullswater	17·0	Brown	—	10·56	4
6	Low Wray Bay	3·0	Dark grey	*Potamogeton perfoliatus*	11·66	4
7	Low Wray Bay	3·5	Black	*P. perfoliatus*	14·24	4
8	Windermere	50·0	Black	—	16·84	4
9	Coniston	8·0	Black	—	18·08	1
10	Esthwaite	3·5	Black	*Potamogeton* spp., *Hydrilla, Naias*	20·64	4
11	Esthwaite	12·0	Black	—	21·34	4
12	Pullwyke Bay	1·5	Brown	*Sparganium, P. alpinus*	26·34	4
13	Esthwaite	1·5	Brown	{*Sparganium* r, *P. obtusifolius* r}	27·32	1
14	Congo Bay	2·0	Brown	*P. perfoliatus*	29·98	4
15	Three Dubs Tarn	1·0	Brown	*Carex* spp.	38·35	3
16	Pullwyke Bay	1·0	Brown	Sterile	42·36	4
17	Three Dubs Tarn	1·0	Black	*Typha angustifolia*	67·89	4

smell similar to sulphuretted hydrogen is produced by many seaweeds due to formation of methyl sulphide. Birge & Juday (1911) have discovered small traces of sulphuretted hydrogen in American lakes at great depth. This gas also occurs in the abyssmal regions of the sea. But in fresh water the concentration of the gas seems to be insignificant, although possibly harmful quantities may sometimes be locally produced.

But the presence of sulphides in the substratum may be indirectly harmful to plant growth through their chemically reducing properties. It is on this account perhaps that Robinson (1930) states that they are harmful to plant growth. Longwell & Pentelow (1935) have shown their harmful effect upon trout. However, in these lakes the aquatic plants seem to be little affected by the presence of sulphides in the muds.

Available nitrogen in the substratum

Waterlogged soils do not normally produce any nitrate. This is true in the case of aquatic muds, since no nitrates could be detected in a number of samples with varying organic content when treated with either diphenylamine or phenol-di-sulphonic acid. It is in fact unlikely that any nitrate should be formed under extremely reducing and anaerobic conditions such as have been shown to obtain in the mud. Thus aquatic plants do not utilize nitrates but ammonia. It has, indeed, been found in laboratory culture experiments that *Potamogeton alpinus* seedlings died very quickly when supplied with nitrogen in the form of ammonium nitrate. On the other hand, active ammonification is known to exist in the mud (see p. 423).

An accurate estimation of ammonia in soils has always been a difficult problem, owing to the fact that ammonium ions are strongly adsorbed by the

soil colloids. Therefore, the extracting reagent and its concentration control the amount of ammonia obtained from a given type of sample. Moreover, many nitrogenous compounds are decomposed easily when the extracting reagent is an acid, so that the amounts of ammonia extracted from a sample of mud tend to increase with increasing concentration of acid.

In order to estimate ammonia in the muds under such circumstances McLean & Robinson's (1924) method was employed. In this method a normal solution of sodium chloride is used for the extraction. The extract is later on distilled with magnesium oxide and the ammonia liberated is determined from the distillate. The results obtained for three typical examples of mud are given in Table VIII, and with them, for comparison, data from an upland *Eriophorum* peat from Ingleborough.

Table VIII

Sample no.	Locality	Vegetation	Organic content % of dry wt.	Ammonia in mg. per 100 g. dry sample
71	Fisherty How Bay	*Isoetes*	8·04	0·7348
24	Low Wray Bay	*Potamogeton perfoliatus*	14·24	4·6610
35	Pullwyke Bay	*Sparganium, P. alpinus*	26·34	2·6160
Peat	Ingleborough	*Eriophorum vaginatum*	96·72	6·1100

Although the limited data do not permit any generalization yet it is suggestive that the most fertile mud (that with *Potamogeton perfoliatus*) gives off the largest amounts of ammonia. This soil then tends to retain available ammonia and the most organic soil tends to lose it. This agrees with the experiment on p. 423 and also with the drift in C/N ratios.

Exchanges between mud and water

Various attempts were made to study the effects of the anaerobic conditions. The most informative type of experiment was based on the fact that the muds rapidly remove oxygen from the water. Hence it is possible and profitable to study the changes in soluble substances in water kept in contact with mud. For this purpose 250 c.c. of three mud types (Table IX) and 700 c.c. of distilled water with each type of mud were placed separately in seven 1 l. flasks with a thin film of paraffin oil upon the surface of the water. Tubings for siphoning out water from the flasks without disturbing the contents inside them were fitted in each of them. All of these flasks were placed under identical conditions of light and temperature in the laboratory. At the end of every week water was

Table IX

Sample no.	Locality	Vegetation	Fresh wt. in g.	Organic content % of dry wt.	Mud type
2	Fisherty How Bay	*Littorella-Isoetes*	429·8	7·34	I
24	Low Wray Bay	*Potamogeton perfoliatus, Nitella*	347·8	14·24	II
35	Pullwyke Bay	*P. alpinus, Sparganium*	362·9	24·34	III

siphoned out from three of the flasks which contained one of each of the types of mud. For determination of oxygen the water was siphoned through a rubber tube discharging it at the bottom of a 50 c.c. flask which was stoppered soon after an excess of water overflowed from the top. It was "winklered" and titrated immediately afterwards.

The concentrations of oxygen and phosphates in the water at the ends of the first two weeks are shown in Table X. The amounts and changes in the concentration of free and bicarbonate (half-bound) carbon dioxide and dissolved ammonia and drifts in *p*H values of water in the three series of flasks are plotted in Fig. 2. Although no algae could be detected growing in the

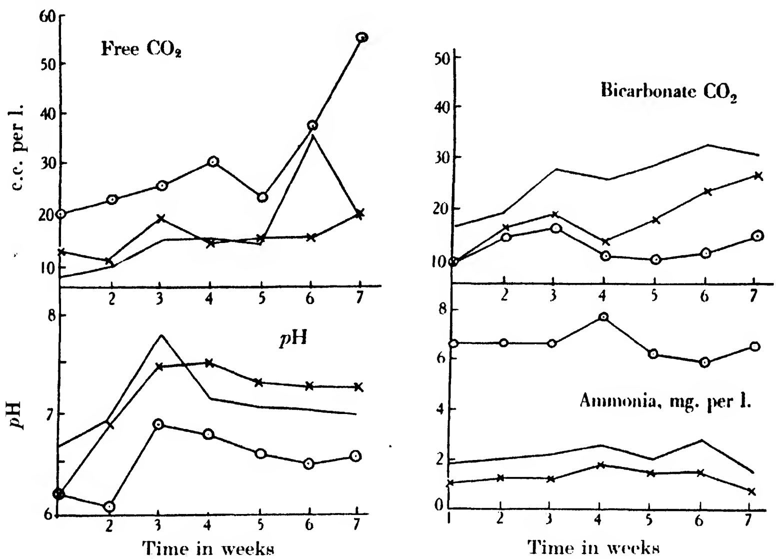

Fig. 2. Mud types: I, crosses; II, plain line; III, circles.

flasks while the experiment was in progress yet absence of minute forms cannot be guaranteed.

Table X

Concentration of gases in the original water (c.c. per l.): oxygen = 5·036; CO_2 = 2·224.

	Oxygen c.c. per l. at the end of		PO_4 mg. per l. at the end of	
Mud type	1st week	2nd week	1st week	2nd week
I	0·6596	0·2087	0·180	0·000
II	0·4656	0·3412	0·460	0·000
III	0·6984	0·0155	0·900	0·100

The following conclusions are obvious from the data presented in the table and the figure:

(1) The organic mud of Pullwyke Bay produced the largest amount of carbon dioxide. This is in general agreement with previous experiments. But

the amount of half-bound carbon dioxide from this type of mud is the *least*. This presumably shows lack of bases which could form stable bicarbonates.

(2) Ammonia produced by the muds in water is proportional to their organic content; but since there is not much change in its concentration in the water after one week it is believed that ammonification stops under extremely anaerobic and toxic conditions such as seem to have existed in the flasks.

(3) The hydrogen-ion concentration of the water is lowered by the decaying underlying muds. A rise of pH to its maximum is observed at the end of three weeks, after which there is a gradual fall; but the final value at the end of seven weeks is still higher than the original in all the three cases. To some extent the pH drifts correspond with free CO_2 variations but the relationship seems to be by no means simple.

(4) Oxygen is consumed very rapidly in all the three cases. The rate of absorption, however, cannot be compared for the three samples since data within the first seven days were not obtained and those at the end of this period cannot be regarded with much confidence due to experimental error at such low concentration of the gas.

(5) Phosphates at the end of a week are found to be directly proportional to organic content of the mud, but they soon disappear by the end of the second week, presumably due to adsorption.

(6) No nitrate in the water could be detected in any case. However, Dr C. H. Mortimer has since observed a small amount of nitrate production at the beginning of a similar experiment.

At the end of the seventh week the water in each case was analysed for iron, aluminium, manganese and calcium. The results are expressed in Table XI as mg. per l. of water.

Table XI

Mud type	Sample no.	Fe*	Al	Mn	Ca
I	2	0·173	58·33	5·887	38·590
II	24	4·760	67·89	4·121	47·180
III	25	32·000	78·74	0·824	2·144

* Fe present as ferrous iron (no reaction for ferric iron obtained with potassium ferrocyanide or potassium thiocyanate).

From this it will be seen that a larger amount of iron and aluminium and a less amount of calcium and manganese are leached out from the more organic mud than from samples containing less organic matter. According to Robinson (1930), who has studied some chemical phases of submerged soil conditions, such solutions contain a large amount of iron and manganese as protobicarbonates. The large amount of carbon dioxide present in the type III sample seems to have been combined with these bases in some such manner. The same author explains this phenomenon as being due to activity of bacteria on organic matter whereby a large amount of carbon dioxide is produced.

It is necessary at this place to consider briefly the system concerned in the above experiment. The source of the elements dissolved in the water is the inorganic and organic matter of the mud. As the organic nitrogen is decomposed the ammonia formed will tend to be adsorbed on the surface of the soil colloids and will replace other ions from these surfaces. The bases exchanged in this way would tend to go into solution combined with any available acid radicles. This solution would be more or less concentrated in the mud being continuously replenished around the mud particles. It would then gradually diffuse out into the aqueous system lying above the mud. The differences in the composition of the supernatant water in the experiment thus represent indirectly the conditions in the soil solution, and it seems clear that the more organic muds must be comparatively deficient in calcium (and other monovalent or divalent bases) and relatively rich in iron and aluminium. In any case it appears that loss of bases from aquatic muds must be the result of the production of ammonia and the leaching effects due to this production.

So far the conditions of the experiment are very similar to those in the lake. But in the littoral region of a lake there is always some supply of oxygen in the water which would oxidize the ferrous iron (or manganous manganese) and thus precipitate it presumably in the form of ferric hydroxide. Peaty muds in sheltered bays where wave action is not vigorous can be seen very often covered with a film of scarlet limonitic scum. According to Caspari (1910) this oxidized form of iron again goes into solution in a ferrous state under reducing conditions and may be reprecipitated when supplied with oxygen. Thus he thinks that iron works to some extent as an oxygen carrier in the breaking down of vegetable debris.

5. EXCHANGEABLE BASES IN LAKE MUDS

The results of the experiments quoted in the last section clearly focus attention upon the minerals present or available in typical samples of mud.

Whatever may be the mechanism of absorption of salts by plants, it is clear that all the minerals present are not available to plants and secondly, that the ions adsorbed on the soil colloids are probably those of greatest importance to plant growth. Thus the mineral properties of a soil are now usually studied by determining the exchangeable bases.

When a soil is shaken with an excess of a neutral salt solution an almost instantaneous ionic interchange between the two systems takes place. So that if it is shaken with a concentrated solution of potassium or sodium chloride the kations $K^{\cdot}$ or $Na^{\cdot}$ are adsorbed upon the colloidal surface of the soil and an equivalent amount of kations such as $Ca^{\cdot\cdot}$, $Mg^{\cdot\cdot}$, $Fe^{\cdot\cdot\cdot}$, etc., is released from the soil into the solution.

In the present case a normal solution of ammonium chloride was chosen as the leaching reagent for the following reason. It has been already explained that organic nitrogen is transformed into ammonia due to its anaerobic

decomposition in the mud and that this ammonia is presumably adsorbed by the colloidal mud particles. It seemed very likely that the NH_4 ions thus adsorbed upon the surface of the mud particles will replace some of the kations already present there. Thus ammonium chloride solution has been employed to imitate the natural process of leaching already going on in the muds. The data for a number of typical soils are given in Appendix IV.

(1) *Exchangeable calcium*

Data for exchangeable calcium obtained for a number of samples are plotted against their humus content in Fig. 3. An arbitrary line has been

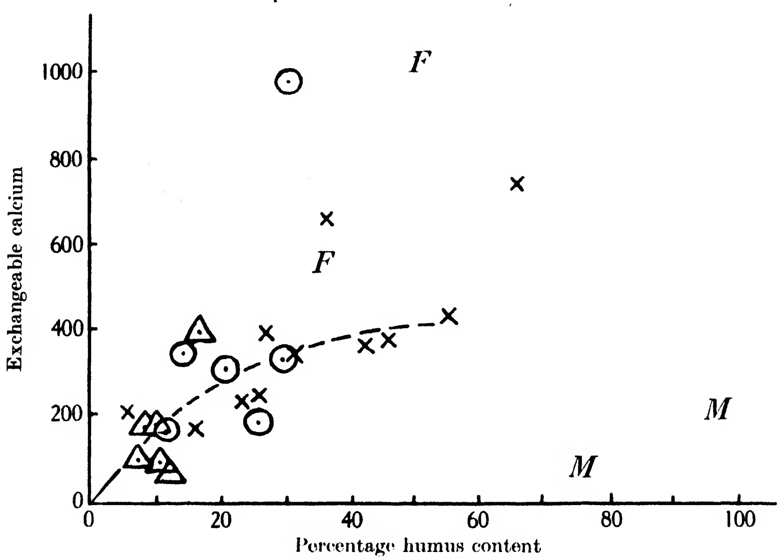

FIG. 3. Exchangeable calcium in muds in relation to the organic content. Triangles represent muds bearing *Littorella-Isoetes*; circles are for *Potamogeton perfoliatus* and *praelongus* muds; crosses for other species. *F* represents "fen" and *M* moor.

drawn in this figure to indicate what seems to be the most usual relation between calcium and humus—that is in the normal plant succession.

One sample at the top of the figure, no. 25, is neglected as it is from a highly silted area (and is also for *Potamogeton praelongus*) but this shows a divergence from the normal rather similar to two figures available for "fen" soils with a luxuriant vegetation, also included in the figure. In contrast are comparable results for two moorland soils—one of cotton-grass peat—both of which show a remarkably low calcium/humus ratio. Obviously, wide variations are possible, due particularly to differences in silting intensity and it is not possible to relate the replaceable calcium to the plant succession. On the other hand the data suggest that the increase in available calcium is related to plant colonization and to increasing organic matter.

(2) *Exchangeable hydrogen*

The amounts of exchangeable hydrogen for five typical samples of mud are given in Table XII with their percentage organic content and the dominant plants they bear in nature. It will be seen from the table that the sterile peaty mud has a high replaceable hydrogen content, almost of the same order as for a peat sample obtained from cotton-grass moor on Ingleborough (700 m.) analysed for the sake of comparison. Of the other four types the two samples bearing *Potamogeton perfoliatus* as their dominant plant represent, no. 24, a typical inorganic *P. perfoliatus* mud and, no. 28, the most highly organic sample for this species. This last one is from a place where the rate of silting is very high, so that it is not representative of the normal succession. These have the least amount of replaceable hydrogen observed whereas *Littorella-Isoetes* and *Sparganium minimum-Potamogeton alpinus* muds have higher values. This shows that *Potamogeton perfoliatus* muds are saturated with other bases than hydrogen, while both typical inorganic and more peaty muds are poor in these other bases. The figures for "exchangeable calcium" are given for reference.

Table XII

No.	Locality	Vegetation	Organic content % of dry wt.	Hydrogen replaced mg. per 100 g.	Exchangeable calcium mg. per 100 g.
7	Fisherty How Bay	*Isoetes-Littorella*	8·04	94·5	171
24	Low Wray Bay	*Potamogeton perfoliatus*	14·24	29·9	342
28	Congo Bay	*P. perfoliatus* (silted)	29·98	16·3	330
35	Pullwyke Bay	*Sparganium*, *P. alpinus*	26·34	75·8	245
85	Pullwyke Bay	Sterile subaqueous peat	42·36	402·8	356
—	Ingleborough	*Eriophorum* peat	96·72	494·3	198

(3) *Percentage base saturation*

Similar conclusions to those shown above are arrived at by calculating the percentage base saturation for these samples (after Hissink's method, 1924–5) as tabulated below:

No.	Percentage base saturation
7	8·35
24	36·40
28	50·40
35	13·95
85	4·25
Peat	2·10

(4) *Exchangeable iron, aluminium and manganese*

The amounts of exchangeable iron and manganese are negligible in inorganic soils (stage I of the succession). They tend to become high in the more organic muds—but there is no sign of a difference between the second and third stages of the plant succession.

Exchangeable aluminium shows a good deal of variability, but on the whole tends to be higher in the second (*Potamogeton perfoliatus*) stage of mud development. The general trend of change for available ions is probably most clearly shown by this summary (Table XIII) for the six typical soils most fully investigated (see earlier tables).

Table XIII. *Exchangeable metallic ions in typical muds*

(mg. per 100 g. of dry soil)

Sample	Organic matter %	Calcium	Iron	Manganese	Aluminium
2	7·3	97	1	0	1
7	8·0	171	1	0	1
24	14·2	342	19	121	11
28	30·0*	330	333	7	24
35	26·3	245	272	2	1
85	42·4	356	278	22	0

* Heavily silted.

The results of these estimations suggest that the greater fertility of the *Potamogeton* soils (Type II) may well be due to the greater amount of exchangeable mineral ions which seem to be present in the more organic muds. The increasing sterility of the most organic muds (Type III) is, however, not easily explained on the basis of these figures, except by assuming that the high proportion of replaceable hydrogen leads to sterility. On the whole, the results of the examination of the ions replaced by normal ammonium chloride solution are somewhat disappointing. It seems probable that the method of standing the muds in water, described earlier, is more suitable for the comparison of ions available to plants, because in this case the leaching agent is the ammonia produced by the activity of the soil itself and hence the replaced ions are the result of both the biological and colloidal properties of the mud. Accepting this point of view, it is concluded that a decisive difference exists between the muds of the second and third types (see Table XI). It may also be concluded that the high fertility of the *P. perfoliatus* type of mud is associated both with a higher proportion of available ammonia (probably a high *rate* of production) and also with a higher degree of saturation with bases (Tables VIII, XII *et seq.*). On the other hand, the sterility of the most organic muds may be ascribed to the low proportions of available calcium and the high proportions of iron under "natural" leaching conditions, as well as to the high exchangeable hydrogen.

6. Analyses of plants

This point of view is supported by the results of ash analyses on the plants. A large number of analyses of representative samples of different species is incorporated in Appendix VI. These are available for reference and they could probably be discussed in many ways. For the present, however, it must suffice to consider three points only.

In the first place, we may consider the composition of the ash of the species growing on the soils most fully examined and most frequently mentioned above. The analyses are brought together in Table XIV, which shows clearly two points, both of which can be verified from a more extensive examination of the data. The plants from the most organic soils (*Sparganium* and *Potamogeton alpinus*) contain very high proportions of iron. The plants of the second or intermediate group of soils (*P. perfoliatus* and *Nitella*) contain much higher proportions of nitrogen than do those growing on the other soil types. Thus, the ash analyses appear to reflect the differences demonstrated in the last section for the different soil types. In short it appears possible that *Sparganium* and *Potamogeton alpinus* survive on soils of the most organic type by virtue of their lower nitrogen requirement and their capacity to withstand high ferrous iron supplies in the soil.

Table XIV

	Littorella	*Isoetes*	*Potamogeton perfoliatus*	*Nitella opaca*	*Sparganium minimum*		*Potamogeton alpinus*
Soil no.	2	7	24	24	35	85	35
Ash	14·66	16·82	17·59	23·64	26·92	21·65	27·49
CaO	1·67	0·74	2·01	1·73	2·78	1·23	1·49
MgO	0·47	0·46	0·73	0·36	0·41	0·47	0·15
Fe_2O_3	0·29	0·39	0·46	0·85	4·16	6·25	6·20
Mn_3O_4	0·05	Tr.	0·02	0·04	0·04	0·19	—
Al_2O_3	1·37	2·30	1·57	1·79	1·09	2·00	1·72
Total N	2·80	2·76	6·25	7·09	4·97	3·28	4·74

Secondly, the data may be analysed in another way—by considering the changes in calcium or iron content in relation to the organic content of the substratum. The data only suffice to indicate this for two species, *Potamogeton perfoliatus* and *Sparganium minimum*, and they are presented in Fig. 4. The percentages of both calcium and iron tend to rise in *Potamogeton perfoliatus* with increasing soil organic content, but there are signs that the calcium content may fall when the organic content of the soil is above 25 %. This fall is shown clearly for *Sparganium* and it is worth emphasizing the corresponding steeper slope of the graph for iron absorption, which suggests that there may be an inverse connexion between the amounts of iron and of calcium taken in. If the isolated data available for other submerged *Potamogeton* species (in Appendix VI) are compared with the curves for *P. perfoliatus*, it is obvious that they differ (at any given *soil* organic content) in having a higher or a lower calcium content than *P. perfoliatus*. It is noticeable that if the calcium content is lower, the iron content is much higher and, vice versa, if the calcium content is higher the iron content is much lower. The latter state is shown in *P. praelongus* and *P. zizii*, both of which characterize inorganic and much silted habitats. *P. obtusifolius* and *P. alpinus* are particularly characteristic of organic soils and have a high iron/calcium ratio. *P. lacustris* and *P. heterophyllus* also tend in this direction. The suggestion clearly is, therefore, that a high iron absorption cuts down the absorption of calcium or vice versa. Taking

it on the whole, then, there are clear indications that the mineral absorption is affected by the soil type and the effects observed are in agreement with the information as to the readily available ions.

A third feature of the analyses is their possible relation to the nitrogen content of the soil and to nitrogen absorption. This possibility may exist for

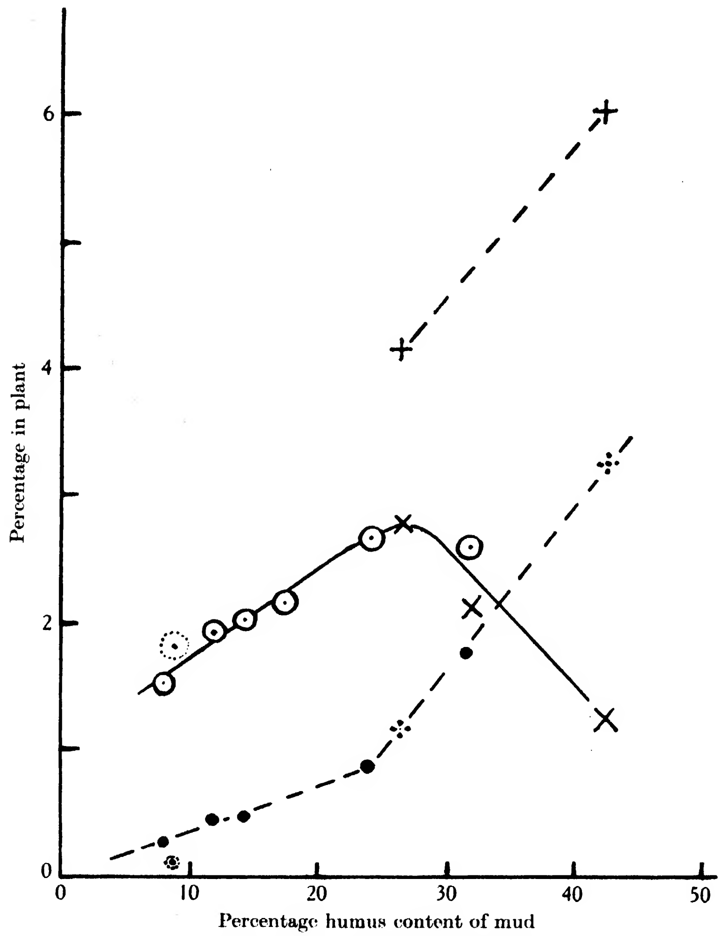

FIG. 4. Relation between calcium and iron absorbed by plants, and humus content of mud. Continuous line, calcium; dotted line, iron; circles, *Potamogeton perfoliatus*; crosses, *Sparganium minimum*.

two reasons. First, the availability of ions from the soil is ascribed to leaching by ammonia (p. 426) and, secondly, a connexion of both calcium and iron with nitrogen metabolism has often been suggested. The curves in Fig. 3 would not be greatly altered if the nitrogen content of the soil were used as base line instead of organic content. But the relation between the plants and the soil type is most clearly shown if we compare, as in Fig. 5, the nitrogen content

of the plants with that of the soils. There is in this figure a clear indication of the greater availability of nitrogen in the soils of intermediate type (nitrogen content ± 0·5 %) with a definite fall in the more organic soils (nitrogen content + 0·9 %). This again agrees with the data for soil properties given earlier (p. 422) for it was shown that available ammonia was highest in the second or intermediate type of soil.

It should perhaps be pointed out that plants with emergent shoots or floating leaves appear to be much less affected by the nature of the substratum.

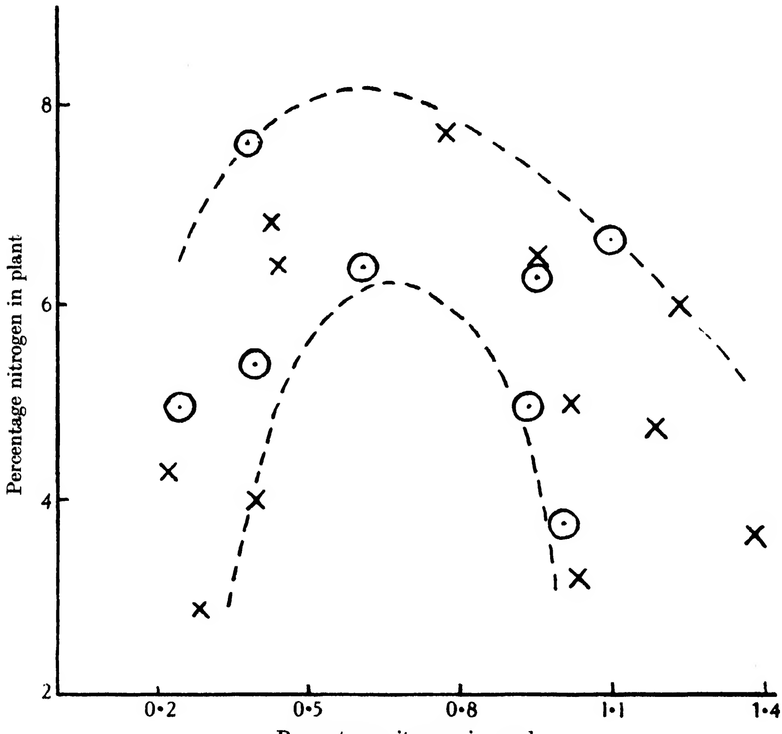

Fig. 5. Relation between nitrogen in plants and nitrogen in muds. Circles for muds bearing *Potamogeton perfoliatus* (and *praelongus*); crosses for other species present.

Further, the analyses given in Appendix VI show that the iron/calcium ratio of the ash in such plants tends to be comparatively low. In this connexion especially it should be remarked that *Sparganium minimum* is usually wholly submerged in the habitats described here.

7. Ammonium-thiocyanate test and the reducing power of lake muds

Determination of exchangeable bases is usually a lengthy process. In an extensive ecological work therefore a field test showing the balance between

exchangeable kations like $Ca^{\cdot\cdot}$ and $K^{\cdot}$ and $Fe^{\cdot\cdot\cdot}$ and $Al^{\cdot\cdot\cdot}$ would be undoubtedly very useful. Comber (1920) devised such a method known as ammonium-thiocyanate test which he employed with agricultural soils in order to find their lime deficiency.

In this test, soil is vigorously shaken with a saturated alcoholic solution of ammonium thiocyanate. Development of red colour in the solution indicates that the soil is sour or base deficient. This conclusion is based upon the principle of base exchange, according to which NH_4 ions of the reagent replace the adsorbed ions of $K^{\cdot}$, $Ca^{\cdot\cdot}$, $Fe^{\cdot\cdot\cdot}$, etc., from the surface of the soil colloids. Soils poor in the mono- and divalent ions will evidently release $Fe^{\cdot\cdot\cdot}$ and $Al^{\cdot\cdot\cdot}$. Aluminium thiocyanate will in such cases be insoluble in alcohol whereas ferric thiocyanate will produce the red colour in the solution.

When Comber's test as outlined above was applied to lake muds poorer in $Ca^{\cdot\cdot}$ and richer in $Fe^{\cdot\cdot}$ it failed to give any colour with them. It is easy to see the reason in light of the present work. The failure of the test is due to absence of ferric iron in muds (cf. p. 424). Thus the test had to be modified in order to apply it to lake muds. The modification consists of shaking a little of the mud with the reagent and when the mud particles settle down at the bottom of the test tube a drop of hydrogen peroxide is added to the solution. This oxidizes ferrous iron to ferric iron and therefore produces the maximum colour almost instantaneously.

This modification of Comber's test has been used in the present study also to compare the reducing power of muds which for the sake of brevity has been called "Reductivity". Obviously a soil containing only ferrous ions must contain reducing processes which maintain a high Fe^{++}/Fe^{+++} ratio. As the thiocyanate solution is normally pink, some of the mud samples appear to show some red colour of ferric thiocyanate with Comber's test when the ferric iron in the reagent is not adsorbed. If the intensity of this original colour be compared with the intensity of the final colour produced after adding hydrogen peroxide to the same solution, a rough measure of the iron present in the reduced condition is obtained. Since only iron is taken into account in this test a wholly negative result does not indicate the absence of reductivity in a

Table XV

No.	Locality	Vegetation	Organic content % of dry wt.	Comber's colour: Without H_2O_2	Comber's colour: With H_2O_2	Reductivity
48	White Cross Bay	*Phragmites*	3·90	±	±	0
7	Fisherty Bay	*Isoetes-Littorella*	8·04	+	+	0
2	Fisherty Bay	*Littorella*	7·34	±	±	0
1	Low Wray Bay	*Littorella-Isoetes*	9·92	±	±	0
24	Low Wray Bay	*Potamogeton perfoliatus*	14·24	—	+ + +	4
27	Esthwaite	*Hydrilla, Potamogeton* spp.	20·64	—	+ + + +	5
35	Pullwyke Bay	*Sparganium, P. alpinus*	26·34	—	+ + + +	3
82	Pullwyke Bay	*Carex, Equisetum*	36·68	—	+ + +	4
76	Three Dubs Tarn	*C. elata*	38·35	—	+ + + + +	6
92	Blelham Tarn	Peat deposit	66·00	—	+ + + + +	6

given mud, but merely shows that the soil is saturated with mono- and divalent bases.

A large number of results obtained with the modified Comber's test for comparative deficiency of bases other than iron (and aluminium) and the reductivity for these mud samples is recorded in Appendix II. A few representative types are given in Table XV, and the general conclusion drawn is that as the lake substratum becomes older and more organic it becomes poorer in mono- and divalent ions, richer in ferrous iron and also becomes strongly reductive. This development distinguishes soils of the first inorganic type from all others.

Oxidation-reduction potential

Emphasis has been laid upon the fact in the foregoing pages that partial and complete anaerobic conditions prevail in the lake bottoms. As a result ferrous iron, sulphides, marsh gas and ammonia may accumulate in the substratum, depending largely upon the activity of the micropopulation. It seems very likely that muds so chemically reduced might also influence the life of rooted plants in general. Therefore, a measurement of this factor, viz. the chemical state of the substratum with regard to oxidized or reduced substances present in it, becomes an immediate problem. Comber's test in its modified form answered the purpose to some extent; but it has the disadvantage that reductivity of samples rich in calcium and potassium (in comparison with iron) could not be estimated by this test.

In recent years measurements of oxidation-reduction potential have been made upon soils. These measurements are based upon the electrical conception of oxidation and reduction. For instance, in the case of iron salts,

$$Fe^{+++} + 1 \text{ electron} \rightleftharpoons Fe^{++}, \qquad \text{(i)}$$

that is, oxidation means liberation of electrons and reduction a gain of electrons. Thus it is assumed that in a reversible system as above there is an electron-escaping and an electron-absorbing tendency. If an inert electrode is inserted in such a system it acquires an electric charge. A measurable potential will therefore be set up if this system is connected with a standard source of potential such as a normal hydrogen electrode. This potential when expressed in volts has been called E_h (cf. Michaelis, 1936).

The E_h of a given system depends primarily upon the concentration of the oxidant to reductant and also on the physical constants of the system. The E_h of a system is known as E_0 when the concentration of oxidant and reductant is 50 % each. Now as given by Clark (1928)

$$E_h = E_0 - \frac{RT}{nF} L_n \frac{(\text{Ox})}{(\text{Red})}, \qquad \text{(ii)}$$

where R = gas constant, T = the absolute temperature, L_n = Naperian logarithm, F = the farad, n = number of electrons transferred in the reaction formula, and (ox) and (red) = concentrations of oxidants and reductants.

But E_h also depends upon the hydrogen-ion concentration of the system, since pH in such systems controls the concentrations of oxidant and reductant by influencing their degree of ionization. Therefore, E_h values obtained from systems like soils with variable pH are not necessarily comparable. To overcome this difficulty Clark introduced the rH scale. On this scale the intensity of the reaction in a given system is expressed as a logarithm of the reciprocal of a hypothetical hydrogen pressure, i.e. $r\text{H} = (-\log \text{H}_2)$, where H_2 is the theoretical pressure of hydrogen. As a matter of fact it is possible to consider a redox system as one which is producing hydrogen by virtue of which reduction takes place. In practice the rH value may be obtained as

$$r\text{H} = \frac{E_h}{29} + 2p\text{H} \text{ in millivolts at } 18^\circ \text{ C.}$$

Thus it corrects for the pH of the medium.

As both the theory of these measurements and also the precautions usually necessary have been discussed at some length recently (Pearsall, 1938), it is possible to dispense with further descriptions. The method used was as follows.

A bright clean platinum electrode was inserted into the sample so collected. This electrode was connected with a saturated potassium chloride-calomel electrode for reference as the standard electrode. The circuit of the cell was made complete through a potentiometer fitted with a tap key. An opposite standardized current ran through the instrument from a 1 V. dry cell. The potential difference between the soil system and the standard electrode was then measured in volts by adjusting the resistance scale to null point. The final value for E_h was obtained by adding 0·25 V. to these readings since that is the difference of potential between the standard calomel electrode and a normal hydrogen electrode at 20° C. pH of the samples was also found by the quinhydrone method. rH values were then calculated from these data by using the formula $r\text{H} = \frac{E_h}{0{\cdot}029} + 2p\text{H}$ as given before.

It must be remembered that whatever precautions may be taken there is always some chance of exposing the mud sample to water containing air while collecting it. Further the material is almost scraped from the bottom when collecting so that only its surface layer is obtained. When it is placed in a container with water on the top and taken to a laboratory for E_h measurements, it may differ from its natural state in the lake in following respects: (1) differences in temperature and pressure, (2) a readjustment of the micropopulation under the new conditions, (3) more oxygen available through the thin film of water on the surface of the mud, (4) continuous leaching of bases from deeper parts of which the movement of iron is especially noticeable. It oozes out of

the mud in the ferrous condition and is precipitated as a red-brown scum on the mud surface in the ferric state, presumably being oxidized by air dissolved in water. This is more obvious in peaty muds since more iron is present in these. Dr C. H. Mortimer has since found that the modified thiocyanate test (p. 432) shows wholly ferrous iron below the mud surface and mainly ferric iron at the surface. In a similar manner the surface film only contains nitrate and the deeper layer no nitrate.

About 1500 c.c. of two mud samples (Table XVI) were collected and each placed in a jar with 500 c.c. of lake water. The containers were then taken to the laboratory without much disturbance. In each of the jars two clean platinum electrodes were suspended, one just at the surface layer of mud and the other at 5 cm. depth from it. E_h readings were then taken at definite intervals of time.

Table XVI

Sample no.	Locality	Organic content % of dry weight
2	Fisherty How Bay	7·34
35	Pullwyke Bay	26·34

Potentials in surface muds

The rH values for the surface electrodes are plotted against time in Fig. 6. It will be seen that a minimum value is obtained for each at about 2 hr.—after which time the rH drifts back. In drifting back values of rH above 22 are obtained after 100 hr. and the third sample records a more oxidizing potential than the first after 126 hr.

It is clear from this that the samples attain an equilibrium in about 2 hr. during which time there is a fall in rH value. The minimum value obtained at this time would correspond to some extent to actual lake conditions. This minimum is proportional to the organic content of the mud. But there is a continuous process of oxygen absorption going on in the mud from the overlying water and so the potential drifts back to higher values. The more organic mud becomes ultimately more oxidizing which seems to correspond with a larger amount of iron present in it. This iron could be seen forming a red-brown scum on the mud surface and is certainly oxidized to ferric state. Hence, it is clear that potential drifts in the surface layer of the mud are due to gradual oxidation in which iron seems to play an important part. The reader may be reminded at this stage that it is the concentration of oxidant to reductant such as that of ferric to ferrous iron which is indicated by oxidation-reduction potentials.

Potentials below the mud surface

Fig. 6 shows rH drifts against time obtained at 5 cm. below the surface of the same two samples of mud. It will be seen that there is no drifting back of rH as seen for the surface layer of the mud. Allowing for slight fluctuations which might be due to temperature differences and biological activity the rH

values seem to keep fairly constant after 2 hr. up to 2 days. Lower values are obtained than the minima recorded for the surface layer of the corresponding samples. These again seem to be proportional to organic content of the mud and would resemble more the natural state obtainable in the mud at the lake bottom. Data obtained after a very long time are not trustworthy since by that time the biological population might entirely change.

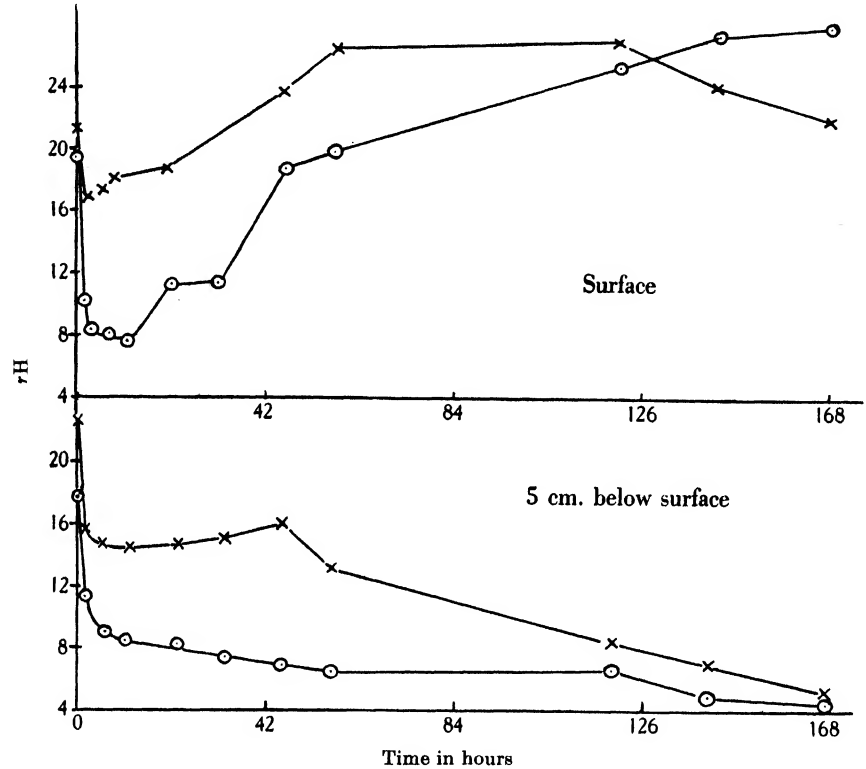

FIG. 6. Drifts of oxidation-reduction potential with time of an inorganic (×) and an organic mud (⊙) at and below the surface. (See text.)

Table XVII shows *r*H drifts for two hours for the following deep-lying mud samples.

Table XVII

Lake	Depth in m.	Organic content % of dry wt.	*r*H at given time in hours 0	0·5	1	2
Ullswater	17	10·56	20·7	15·1	14·4	14·1
Windermere	50	16·84	16·0	12·8	11·6	11·0
Esthwaite	12	21·34	22·8	12·0	7·7	6·9

The minimum *r*H values attained at 2 hr. are roughly inversely proportional to the organic content of the samples. Further, it will be noticed that the curve

is more steep for the muds with low final rH. This is presumably due to the greater capacity of such muds to get oxidized during collection. They then become strongly reducing in a short time. It seems evident then that such muds are strongly reactive and can absorb oxygen from the lake water more rapidly than the others.

Again, similar rH drifts are found for the samples shown in Table XVIII.

Table XVIII. *Drifts in rH values*

Sample no.	Locality	Organic matter % of dry wt.	C/N	rH at given time in hours 0	0·5	1	2
89	Coniston	18·08	14·15	20·6	16·2	13·8	12·0
27	Esthwaite	20·64	9·30	22·0	13·7	10·9	9·5
76	Three Dubs	38·35	20·40	16·0	16·2	16·2	15·9

In these cases the final rH values are not directly proportional to organic content of the samples. On the contrary they tend to be in reverse proportion. If the C/N ratio be taken to represent rate of decomposition of organic matter so that the lower C/N ratios show a higher rate of decay as explained before (p. 417), it might appear that lower rH values are associated with a high rate of microfloral activity and the higher rH values with slow decay and a tendency to form peat. The greater steepness of rH curves for samples having lower C/N values also suggest the same fact.

In fact, the Esthwaite sample (from a place characterized by rapid silting) is probably very active, while the Three Dubs sample is certainly, from other criteria, a most inactive sample of mud.

Thus the data suggest that the drifts of potential or of rH value may be a measure of the microfloral activity—a conclusion reached also by Pearsall (1938) for terrestrial soils on very different facts. A large drift of rH thus suggests an active mud and probably, in nature, the most active decay. The tendency also is for these active muds to have the lowest *rH* values after 2 hr. Thus when we compare the data for rH after 2 hr. for representative muds from the usual plant succession, it is not altogether surprising to find that the rH values tend to vary, being high in the colonizing stage, low in the intermediate *Potamogeton perfoliatus* stage and rising again when the soil is more organic. This is shown in Table XIX.

Table XIX

Stage	Sample no.	pH	E_h (mV.)	rH	Organic content % of dry wt.
I	7	6·64	+151	17·9	8·0
	9	6·40	+172	18·7	10·8
II	24	6·60	− 98	9·8	14·2
	26	6·24	− 84	9·6	11·7
III	34	5·98	+ 72	14·4	27·3
	35	5·77	+ 17	12·1	26·3

The second type of mud is thus presumably the most active in reduction and this agrees with its high available ammonia content (p. 422) and its high fertility.

Discussion

Dachnowsky (1908) and Robinson (1930) attach great importance to reducing properties of aquatic muds rich in organic matter. They think that the large amount of ferrous iron and sulphides present in these are toxic to plants growing upon them. Such may be the case in small ponds under extremely stagnant conditions but the data presented do not show it to be so in the English lakes. The presence of large amounts of marsh gas and presumably some sulphuretted hydrogen may also possibly be injurious to plant growth in localities with peaty mud although it has not proved possible to obtain definite evidence of this.

The data for reductivity, sulphide content and replaceable ferrous iron do not suggest that there is any real difference between moderately organic (type II) and highly organic soils (type III) in these respects, at least by the methods used. The data for oxidation-reduction potentials and for available ammonia focus attention on the greater microfloral *activity* of the moderately organic soils of type II and this is associated in practice with a greater fertility or abundance of vegetation in this stage. Undoubtedly the combined effects of increased organic matter and more silt render muds of this type richer in replaceable bases in general as well as potash (see Pearsall, 1920) and explain the tendency shown for these soils to be most "saturated" with bases by Hissink's method. Finally, the inability of such plants as *Potamogeton perfoliatus* to grow on the most organic soils seems to be associated with a greater availability of iron rather than bases such as calcium as well as with lower availability of nitrogen. This is suggested both by the analyses of plants and also by the "natural leaching" experiment (see Fig. 2).

It is not to be inferred from these conclusions that the distribution of aquatic plants is only controlled by the character of the substratum. Quite clearly factors due to competition and ecesis must also be present and these need some consideration.

The mechanism for the distribution of aquatic plants seems on the whole to be very effective in the sense that it is unusual in a large lake to find what appears to be a suitable habitat which is not occupied by vegetation characteristic of the given type of mud.

According to Dr Pearsall, *Potamogeton perfoliatus* was a rare species in Fisherty How Bay in 1932 at a depth of about 4 m. Now, within a period of four years, this plant has become the dominant species in that area extending up to 6 m. deep water. This colonization is due primarily to the greater clearness of the water in the last four years and the resultant extension of the habitable

zone. But the facts show the efficiency of the colonization mechanisms of such a plant.

The *disappearance* of a plant may sometimes be due to competition. A culture experiment with *Isoetes* on the different types of substrata is very suggestive here. Three seedlings (4–5 leaves and of similar weights in each experiment) were grown for two months on each of four types of mud submerged in large glass battery jars in the lake at a depth of 1·5 m.

Growth of Isoetes lacustris

	Sand	Silt	Black mud	Brown mud
Organic content	Very low	7·3	14·2	26·3
Dry wt. of plants (g.)	0·195	0·212	0·240	0·313

It will be seen that although *Isoetes* can grow better upon organic substrata in culture, yet the plant is not so distributed in nature. It seems, hence, very likely that the plant cannot adjust itself with regard to the changing level of the substratum when silt is being deposited. Practically the whole of its corm remains buried under silt and so it can perhaps do well only at those places where wave action is able to wash away the finer silts deposited or where silt deposition is slow. With the accumulation of organic matter and fine silt upon the substratum *Potamogeton perfoliatus* and *Nitella* spp. also appear in nature and they compete with *Isoetes*. But since the former does not completely cover the ground *Isoetes* may still persist in association with *Potamogeton perfoliatus* for some time. *Nitella*, however, forms a thick mat on the floor and hence *Isoetes* cannot grow with it in abundance. Thus extinction of *Isoetes* is probably brought about by edaphic as well as by competition factors in the English lakes.

Again, in the culture experiments although *Potamogeton perfoliatus* and *P. alpinus* both seem to grow fairly well on an organic substratum yet the latter can do so better than the former if the organic content is more than 15 % of the mud. Thus *P. alpinus* with its habit of rapid spread and better growth on peaty lake floors may obliterate *P. perfoliatus* from such habitats when in competition. In nature very few places are found where *P. perfoliatus* still lingers upon substrata so developed.

It has been said before that *Phragmites communis* can pass through all the stages of the development of lake substratum. This is obviously due to structural adaptations of the plant such as tough rhizomes with remarkable power of spread and well-developed aerial shoots. *Elodea canadensis*, again, is notorious for its spread in fresh-water habitats and seems to tolerate a wide habitat-range. It is not able to compete with the larger *Potamogeton* spp., however, but persists in abundance on organic substrata.

In some cases two similar species do not compete seriously. Thus in Low Wray Bay *Potamogeton perfoliatus* is the dominant plant during the spring and early summer. However, by autumn *P. praelongus* becomes the dominant

plant in the same locality. Thus there appears to be little competition between these two species.

On the whole it seems that edaphic factors control the distribution of aquatic plants in nature. Biological factors as shown above may bring about slight deflexion in the plant successions, but they too seem to be indirectly related to edaphic factors. Thus the replacement of *Isoetes* by *Potamogeton perfoliatus* and *Nitella* through biological competition is brought about by silting effects which promote the growth of these last two plants. A change over in edaphic conditions to the third stage of development of substratum may leave the areas so affected sterile. These sterile regions sooner or later may get colonized by *Potamogeton alpinus* and *Sparganium minimum*.

Summary

1. The distribution of aquatic plants in the English lakes has been studied with particular regard to the nature of the substratum.
2. Physical and chemical characters of the lake muds have been found to be closely correlated with the vegetation on them. This view is supported by suitable culture experiments done in Lake Windermere.
3. The source, its distribution on the lake floor and nature of the organic matter have been given in some detail. A relationship with the quantity of organic matter in the substratum and plant successions has been shown.
4. An analysis of carbon and nitrogen ratio of the substratum shows that in general this ratio is high (12–20) although the ratio for submerged plants is low.
5. Decomposition of organic matter in submerged muds has been shown to be chiefly anaerobic. During this process a large amount of marsh gas and some carbon dioxide are produced. Oxygen if available is rapidly absorbed.
6. Sulphides have been shown to be present in appreciable amounts in practically all the submerged muds containing more than 5–10 % of organic matter.
7. Nitrates are absent from the substratum and nitrogen is available for the aquatic plants in the form of ammonia.
8. A modification of Comber's thiocyanate test has been devised to measure the amount of easily replaceable ferrous iron and the reductivity of the muds.
9. By measurements of oxidation-reduction potential the highest reduction intensities are found to exist in soils of moderate organic content. These are most fertile, contain most available ammonia and the least replaceable hydrogen.
10. The exchangeable bases (with N ammonium chloride) in the muds are related to the organic content of the mud.

In general, a better relation with plant distribution is shown by the bases leaching into water under anaerobic conditions. There is evidence, as the

substratum becomes more organic, of increased availability of calcium and nitrogen. The sterility of the most organic soils is attributed to absorption of ferrous iron and to lower available nitrogen. These conclusions are based also on analyses of plant material.

The author wishes, in conclusion, to express his indebtedness to Dr W. H. Pearsall for his most able guidance throughout the course of this study. He is also grateful to the staff of the Fresh Water Biological Laboratory at Wray Castle, who were always willing to help and give facilities in the field work.

APPENDIX I

Chemical methods

All collections for analysis of plants and muds were done in the months of July, August and September of 1935 and 1936.

Chemical analysis of water

Oxygen. Dissolved oxygen in water was estimated by Winkler's method. This method is given in detail by Birge & Juday (1911). Water-sampling bottle was used for collecting samples and every possible care was taken to exclude air bubbles while collecting them. The samples were "winklered" on the boat and titrated the same day in the laboratory.

Carbon dioxide. Samples of water were collected in the same way as above and titrated as soon as possible against a standard solution of sodium carbonate using phenolphthalein as indicator. The details of the method were followed according to Birge & Juday (1911).

Half-bound and fixed carbon dioxide. These were again estimated by methods given by Birge & Juday (1911) in which the samples were titrated against a standard solution of hydrochloric acid using methyl orange as indicator.

Study of muds

Collection. Mud samples were collected by means of a "Peterson grab". The Peterson grab would not work where the substratum is hard or sandy. Hence an iron hoe attached to a long graduated pole was used in such cases to dig out the bottom mud. Similarly in reedswamp areas a spade had to be used to dig out the subaqueous peat samples from the hard matty substratum formed by rhizomes of the reeds. But in all these cases precautions were taken to expose the samples to the atmosphere as little as possible.

Hydrogen-ion concentration was determined for the mud samples freshly collected. It was done potentiometrically by measuring potential difference between 1 : 3 mud and water solution saturated with quinhydrone and a saturated potassium chloride-calomel electrode. The details as given by Wright (1934) were followed throughout the work. pH is calculated from the formula $p\text{H} = 7\cdot8 - \frac{\text{potential diff.}}{0\cdot058}$ at 20° C.; but in actual practice pH was read directly from the potential difference readings plotted upon a graph for that purpose in accordance with the formula given above.

Nitrates. Qualitative tests for nitrates were made by taking approximately 1 : 2 mud-water extract and treating it with a solution of 0·2% diphenylamine in sulphuric acid. The phenol-di-sulphonic acid method (Harper, 1924) was used in some cases as it was found to be more sensitive and the amount of nitrate could also be estimated accurately.

Sulphides were qualitatively detected by the lead acetate method. It has been slightly modified from Rost's (1922) method and is as follows: 50 c.c. of fresh mud, 50 c.c. of distilled water and about 10 c.c. of sulphuric acid were boiled together in a pyrex flask for 2 min. Filter paper pieces previously soaked in a saturated solution of lead acetate and then dried were applied at the mouth of the flask for exactly 2 min. in every case. The degree of blackening of the paper due to liberation of sulphuretted hydrogen from the mixture and its reaction with lead acetate is expressed in the tables in numbers (1 to 4) representing the intensity of colour.

Adsorbed ammonia. No satisfactory method could be evolved to estimate ammonia content of the mud. The difficulty arises owing to the danger of decomposing nitrogenous compounds during the process. However, McLean & Robinson's (1924) method seemed to be the best under the circumstances and a few estimations were done to obtain comparative values. In this process 100 c.c. of mud were allowed to stand with 200 c.c. of a cold normal solution of sodium chloride overnight. The following morning the solution was filtered and the mud washed with normal sodium chloride solution until 500 c.c. of the filtrate was obtained. The leachate is then distilled with an excess of magnesium oxide into approximately $N/75$ hydrochloric acid solution. Ammonia is estimated by titrating the excess acid with caustic soda solution using methyl red as indicator. Nesseleriation was tried in many cases where the ammonia content of the extract was too small for titrating with the caustic soda solution.

Exchangeable bases. 100 c.c. of mud sample were leached with 500 c.c. of a cold normal solution of ammonium chloride by the usual process (cf. Wright, 1934). The leachate was then concentrated on a water-bath and evaporated with 50 c.c. of conc. HNO_3 to get rid of the ammonium chloride. The bases were then determined according to the following scheme which is based upon methods of quantitative analyses as given by Clowes & Coleman (1909), Wright (1934), Epperson (1928) for magnesium, and Hopkins & Wann (1926) for iron: Add 5 c.c. of conc. HCl to the residue obtained after evaporating the leachate with HNO_3. Evaporate to dryness in a pyrex beaker, breaking flakes at the bottom. Dehydrate at 110° C. for 1 hr. Extract with dilute HCl. Filter through 42 Whatman paper.

(*a*) *Precipitate*: Ignite precipitate and filter paper separately. Weigh them together as SiO_2.

(*b*) *Filtrate*: Add NH_4Cl solution (5 g. NH_4Cl to about 200 c.c. of filtrate), heat nearly to boiling, add NH_4OH solution in slight excess and boil for 1 min. Filter through Buchner funnel with a slight suction. Wash precipitate with 2% cold NH_4Cl solution.

(*c*) *Precipitate*: Dissolve it in a little dilute HCl and reprecipitate as before. Add the previous filter paper as pulp and suck dry on a Buchner funnel. Roll up the filter paper. Ignite in a crucible and weigh as Fe_2O_3, Al_2O_3, Mn_3O_4.[1]

(*d*) Add together filtrates from (*b*) and from (*c*): Add NH_4OH in excess, boil, remove flame then add excess of finely powdered ammonium oxalate. Boil for a minute, cool and allow to settle for 4 hr. Filter, wash precipitate with weak oxalic acid solution.

(*e*) *Precipitate*: Dry and ignite at a high temperature for a long time; cool and weigh as CaO or if too small, dissolve in H_2SO_4 and titrate against standard $KMnO_4$.

(*f*) *Filtrate*: Neutralize, add 5 c.c. conc. HCl and 2 drops of methyl red indicator. Dilute to about 150 c.c. and add 10 c.c. of a saturated solution of di-ammonium-hydrogen-phos-

[1] To separate iron, manganese and aluminium: Dissolve the oxides in warm conc. HCl with a few drops of conc. HNO_3 and make up to 100 c.c. with distilled water. Estimate *iron* colorimetrically in 10 c.c. of the solution. Estimate *manganese* colorimetrically in 10 c.c. of the solution.

Calculate out the amount of Al_2O_3 in the ignited material from the results obtained for Fe and Mn colorimetrically. Jung's (1932) method of estimating aluminium directly was tried for estimating this element when present in very small amounts. It is done by precipitating aluminium by means of 8-oxychinolin.

phate; then add ammonia solution (sp. gr. 0·88) slowly whilst stirring, until the solution is neutral. Stir for 5 min., add 5 c.c. more ammonia and stir again for 10 min. (This is best done in pyrex flasks with rubber stoppers.) Stand for 4 hr. or overnight. Filter. Wash precipitate with 3–5% by vol. of ammonia solution.

(*g*) *Precipitate*: Ignite at low and then at high (1000° C.) temperature to a constant wt. Weigh as $Mg_2P_2O_7$.

(*h*) *Filtrate*: Reject.

For calcium

In case of calcareous muds such as found in Malham Tarn, it is necessary to leach the sample in two 500 c.c. portions and then determine the amount of calcium present in both of the leachates separately. Exchangeable calcium in these cases is equal to Ca present in the first leachate minus Ca present in the second leachate (cf. Hissink, 1924–5).

Exchangeable hydrogen was determined by the method adopted by Turner and followed by De Silva (1934), 100 c.c. of the mud was mixed well with excess $CaCO_3$ and then leached by normal solution of sodium chloride. The amount of calcium in this leachate was determined by the usual method given above. A correction was applied for $CaCO_3$ directly dissolved by the NaCl solution (i.e. 0·028 g. Ca per l. of the leaching reagent). By deducting the amount of exchangeable calcium (previously determined) from the amount of calcium so estimated an equivalent amount of exchangeable hydrogen is obtained.

Percentage base saturation was calculated by Hissink's formula:

$$\text{Percentage base saturation} = \frac{100\,S}{R},$$

when S = total exchangeable calcium expressed as an equivalent amount of hydrogen, T = base exchange capacity or (S + exchangeable hydrogen). All the figures in the above formula are expressed in mg. equivalents per 100 g. of dry weight of the sample.

Humus. Estimated by loss in weight upon igniting the dried sample in a muffle furnace. Half of this value has been taken to represent (roughly) the carbon content of the sample.

Total nitrogen. Estimated by Kjeldahl's method.

Phosphate. Determined by Denige's method as given by Atkins (1924). It was done on aqueous extracts from dried samples.

Chemical analysis of plants

Collection and drying. The plants for analysis were collected from different lakes, washed well to remove mud or sand and spread on paper or hung by means of strings in a dust-free and dry room. In most of the cases they were picked up by their roots, but in the case of reeds and sedges, rhizomes and shoots were collected separately since the proportion of rhizome and root in them is difficult to determine. Precautions were taken to collect the individuals of a species of the same age and at the same time of the year, as far as practicable.

When air dry they were cut into pieces and dried in an oven at 65° C. to a constant weight and finally powdered.

Ashing. 4–5 g. of the dry material in a porcelain crucible was ashed in a muffle furnace at dull red heat to a constant weight.

Total nitrogen. Estimated by Kjeldahl's method.

Crude protein. Calculated by multiplying the total nitrogen value by 6·25.

Ether extract. Estimated by means of a soxhlet extractor with a reflux condenser.

Crude fibre. Estimated by boiling 3–5 g. of the material in 1·25% H_2SO_4 for half an hour and then in 1·25% NaOH after washing again for 30 min. Then it was filtered and washed with 1% HCl, water, 95% alcohol and finally ether; dried to constant weight and ignited. Loss on ignition = crude fibre.

Nitrogen-free extract (soluble carbohydrates) was calculated as = 100 − (% ash content + % crude protein + % crude fibre). The solids dissolved in the ether extract were found to be very small in aquatic plants and so have not been taken into account in calculating out this value.

Ash analysis. Was done for estimating silica, iron, aluminium, manganese, calcium, magnesium and phosphate according to the scheme already given on p. 443.

APPENDIX II

Analysis of mud samples

Sample no.	*p*H	Thio-cyanate	Reduc-tivity	Dried sample: % organic content	Dried sample: % total nitrogen	C/N	Phosphate as PO_4 p.p.m. of dry sample
1	6·74	1/1	0	9·92	0·3953	12·60	—
2	7·30	1/1	0	7·34	0·2792	13·15	—
3	8·00	—	—	9·26	0·2750	16·83	0·0
4	6·82	—	—	6·68	0·2058	16·22	5·0
5	6·86	—	—	7·91	0·1450	27·30	2·0
6	6·82	1/1	0	16·86	1·0890	7·75	—
7	6·64	1/1	0	8·04	0·6175	12·90	—
8	7·41	—	—	6·99	0·2268	15·20	7·0
9	6·40	0/1	2	10·76	0·3703	14·50	—
10	6·44	—	—	20·90	0·7741	13·49	2·0
11	8·00	—	—	14·80	0·6252	11·84	3·5
12	6·68	—	—	10·02	0·3657	13·64	7·5
13	6·60	0/0	0	10·69	0·2698	19·81	3·0
14	6·38	—	—	—	—	—	—
15	6·39	—	—	7·20	0·2165	16·65	2·5
16	5·44	1/3	2	8·66	0·2742	15·80	—
17	6·34	1/3	2	8·68	0·4535	9·70	11·0
18	5·66	—	—	8·04	0·2308	17·42	7·5
19	6·58	—	—	8·56	0·3823	11·21	5·0
20	6·30	—	—	13·40	0·5062	13·23	4·0
21	6·30	—	—	25·84	0·5616	22·97	4·0
22	5·78	—	—	16·42	0·6006	13·66	4·0
23	6·38	0/3	4	11·70	0·3614	15·75	4·0
24	6·60	0/3	4	14·24	0·5853	12·15	—
25	5·90	0/4	5	30·70	1·0890	14·10	—
26	6·24	0/5	6	11·66	0·4229	13·80	—
27	6·62	0/4	5	20·64	1·1170	9·28	4·0
28	5·98	1/4	3	29·98	0·9860	15·20	—
29	5·92	0/4	5	25·28	1·0160	12·45	—
30	7·02	—	—	23·94	0·9203	9·42	6·0
31	5·43	—	—	31·36	0·9313	16·23	5·0
32	6·60	—	—	24·04	0·8074	14·89	4·0
33	6·50	0/5	6	31·12	1·0230	15·20	—
34	5·98	0/1	2	27·32	1·1840	11·50	—
35	5·77	1/4	3	26·34	1·0080	13·08	—
36	6·32	1/3	2	28·68	0·8724	16·50	—
37	5·81	—	—	18·06	1·1760	7·68	9·0
38	5·88	—	—	36·86	1·1280	16·34	4·5
39	5·38	—	—	31·80	1·2190	13·05	7·5
40	6·06	—	—	23·56	0·7636	15·42	4·5
41	6·80	—	—	33·30	1·5570	10·69	2·5
42	6·26	—	—	15·44	0·5611	13·76	9·0
43	6·06	—	—	26·04	1·2180	10·69	6·5
44	5·68	—	—	22·00	0·6797	16·19	5·0
45	7·18	—	—	2·38	0·0550	21·72	3·5
46	6·76	—	—	36·86	0·3864	47·69	12·5
47	5·33	—	—	56·04	1·4760	18·98	—
48	7·50	1/1	0	3·90	0·1299	15·00	—
49	5·93	—	—	13·26	0·5104	13·00	—
50	5·84	1/4	3	—	—	—	—

Sample no.	pH	Thio-cyanate	Reduc-tivity	Dried sample % organic content	Dried sample % total nitrogen	C/N	Phosphate as PO_4 p.p.m. of dry sample
51	6·07	0/2	3	—	—	—	—
52	5·70	0/3	4	—	—	—	—
53	5·97	1/4	3	—	—	—	—
54	5·98	1/3	2	—	—	—	—
55	6·16	0/3	4	—	—	—	—
56	7·10	0/0	0	46·92	1·7630	13·30	—
57	5·84	0/2	3	50·74	0·8487	29·90	—
58	7·40	1/1	0	5·76	0·4501	6·49	—
59	6·62	1/1	0	25·08	0·9389	13·40	—
60	6·29	0/3	4	—	—	—	—
61	6·80	0/1	2	—	—	—	—
62	6·12	0/3	4	23·52	0·8672	13·55	—
63	6·10	0/4	5	—	—	—	—
64	5·86	—	—	32·24	0·9900	16·38	6·5
65	7·20	0/2	3	—	—	—	—
66	5·88	0/3	4	—	—	—	—
67	5·98	0/5	6	—	—	—	—
68	5·80	1/5	4	—	—	—	—
69	5·94	0/5	6	—	—	—	—
70	5·74	1/4	3	—	—	—	—
71	7·08	0/1	2	—	—	—	—
72	6·18	0/2	3	—	—	—	—
73	5·93	0/4	5	—	—	—	—
74	6·82	0/0	0	—	—	—	—
75	5·70	0/1	2	—	—	—	—
76	5·68	0/5	6	38·35	0·9408	20·38	—
77	5·42	1/3	2	—	—	—	—
78	5·58	1/3	2	—	—	—	—
79	5·64	1/2	1	—	—	—	—
80	5·38	1/3	2	—	—	—	—
81	5·80	1/4	3	55·64	1·1820	23·50	—
82	5·88	0/3	4	36·68	1·0250	17·90	—
83	5·78	2/3	1	19·26	0·7539	12·80	—
84	5·79	0/5	6	67·89	1·5520	21·90	—
85	5·60	1/4	3	42·36	1·3740	15·50	—
86	6·08	0/5	6	10·56	0·2989	17·60	—
87	5·67	1/3	2	12·84	0·4506	14·30	—
88	6·56	0/5	6	16·84	0·5384	15·10	—
89	6·20	0/4	5	18·08	0·6400	14·15	—
90	6·48	1/5	4	21·34	0·8539	12·50	—
91	6·38	0/4	5	24·00	1·0280	11·68	—
92	5·92	0/5	6	66·00	1·8200	18·15	—
93	5·84	1/5	4	45·84	1·3710	16·70	—
94	5·76	1/5	4	—	—	—	—

APPENDIX III

Details of mud samples

No.	Lake and depth (m.)	Type of mud	Vegetation
1	W.,* Low Wray, 1·5	Sand, I	*Littorella uniflora* d
2	W., Fisherty How, 1·5	Sand, I	*Littorella* d, *Isoetes lacustris* f
3	Esthwaite, 2	Sand, I	*Littorella* d
4	Coniston, 1	Sand, I	*Littorella* d
5	W., White Cross, 2	Sand, I	*Littorella* d, *Isoetes* a
6	W., Pullwyke, 1·5	Fine silt	*Littorella* a, *Lobelia Dortmanna*
7	W., Fisherty How, 3	Coarse silt, I	*Isoetes* d, *Littorella* a
8	W., Low Wray, 1	Coarse silt, I	*Isoetes* d, *Littorella* f
9	Ennerdale, 10	Sand, I	*Isoetes* d, *Nitella opaca* f

* W. signifies a sample from Windermere, the name of the bay being given subsequently. Abbreviations of plant names are *C.* for *Carex*, and *P.* for *Potamogeton*. Frequencies: d = dominant, a = abundant, f = frequent.

No.	Lake and depth (m.)	Type of mud	Vegetation
10	Derwentwater, 5	Coarse silt	*Nitella* = *Isoetes*
11	Esthwaite, 2	Silt, I	*Isoetes* d
12	Ullswater, 1·8	Sand, I	*Isoetes* d
13	Ullswater, 1·5	Coarse silt, I	*Isoetes* d, *Myriophyllum spicatum* a
14	Coniston, 1·5	Sand, I	*Isoetes* d
15	Derwentwater, 1·5	Coarse silt, I	*Juncus fluitans* d
16	W., White Cross, 1·5	Sand	*Polygonium amphibium* d
17	W., Sawpit, 3·5	Clayey, with bluish to reddish mottlings	*Potamogeton perfoliatus* d
18	W., Fisherty How, 4		*P. perfoliatus* a, *Isoetes* f
19	Ullswater, 2·5	Coarse silt, II	*P. perfoliatus* d
20	Ullswater, 2	Black, semi-liquid, II	*Nitella opaca* d
21	Ullswater, 1	Brown, clayey	*Myriophyllum spicatum* d
22	Coniston, 3·2	Black, semi-liquid, II	*Nitella* d, *P. perfoliatus* a
23	Coniston, 3	As 22	*P. perfoliatus* = *P. zizii* a, *Isoetes* f
24	W., Low Wray, 3·5	As 22	*P. perfoliatus* d, *P. lacustris* f, *Nitella* f
25	W., Congo, 3·5	Brown silt	*P. praelongus* a
26	W., Low Wray, 3	Black, semi-liquid, II	*P. perfoliatus* d, *P. lacustris* a
27	Esthwaite, 3·5	Black, semi-liquid, II	*Naias flexilis*, *Hydrilla verticillata* and *P. crispus* all a
28	W., Congo, 2	Brown silt, II	*P. perfoliatus* d
29	W., Pullwyke, 3	Brown mud, II	*P. perfoliatus* d, *P. lacustris* f
30	W., Pullwyke, 1	Brown silt, II	*P. perfoliatus* d
31	W., Pullwyke, 3	Brown silt, II	*P. perfoliatus* d, *P. lacustris* a
32	W., Congo, 3·5	Brown silt, II	*P. perfoliatus* d, *P. praelongus* a, *P. obtusifolius* f
33	Blelham Tarn, 3·5	Black, semi-liquid, III	*P. obtusifolius* d, *Sparganium minimum* f, *Elodea*
34	Esthwaite, 1·5	Brown mud, III	*P. obtusifolius* = *Elodea* = *Sparganium*
35	W., Pullwyke, 1·5	Brown mud, III	*Sparganium* = *P. alpinus* d
36	W., Congo, 1	Brown mud, III	*Sparganium* d, *P. alpinus* a
37	W., Congo, 0·5	Brown mud	*Chara fragilis* d, *Sparganium* f
38	W., Congo, 0·5	Peaty mud, III	*Sparganium* d, *P. alpinus* f
39	W., Congo, 1	Peaty mud, III	*Sparganium* d, *P. obtusifolius* f
40	W., Pullwyke, 1	Peaty mud, III	*Elodea* d
41	Derwentwater, 3·5	Black, semi-liquid	*Chara* = *Fontinalis antepyretica* d
42	Esthwaite, 3	Brown mud, III	*Fontinalis* d
43	Esthwaite, 3	Black, semi-liquid, III	*Fontinalis* d, *Elodea* f, *P. alpinus*
44	Coniston, 8·8	Black, semi-liquid, II	—
45	W., Sandywyke, 0·5	Sand, I	*Phragmites communis* d
46	W., Pullwyke, 1	Peat in sand, III	*Phragmites* a, *Lobelia Dortmanna* f
47	W., Pullwyke, 0·5	Peaty mud, III	*Phragmites*, *Carex inflata* co. d
48	W., White Cross, 1·5	Sand, I	*Phragmites* a, *Lobelia* f
49	Esthwaite, 3	Much coarse silt	*Nuphar lutea* = *Nymphaea alba* d
50	Esthwaite, 1·5	Brown, III	*Nymphaea* d
51	Blelham Tarn, 2·5	Brown, III	As 50
52	W., White Cross, 1·5	Silt, III	As 50
53	Esthwaite, 2·5	Black, clayey, III	*Nymphaea* d, *Nuphar* f, *Sparganium* f
54	Esthwaite, 1·5	Brown	*Nuphar* d, *Nymphaea* f
55	Ullswater, 1·5	Black, close	*P. natans* d
56	Blelham Tarn, 1·5	Black, clayey	*Phragmites* d
57	Blelham Tarn, 1·5	Black, clayey	*Phragmites* d, *C. inflata* f
58	W., Congo, 0·8	Coarse silt	*Phragmites* d, *Littorella*
59	W., Pullwyke, 1	Silt	*Phragmites* d, *Lobelia* f
60	Blelham Tarn, 0·5	Silt	*Phragmites* d
61	Blelham Tarn, 0·3	Peaty	*Phragmites* d, *C. inflata* f
62	W., Pullwyke, 0·5	Brown mud	*Equisetum limosum* sd, *Lobelia* f
63	Ullswater, 0·5	Black, clayey	*Menyanthes trifoliata* d, *C. inflata* f
64	Ullswater, 0·8	Black, close	*Phragmites* = *P. natans* = *Menyanthes*
65	Esthwaite, 1·5	Black, close	*Scirpus lacustris* d
66	Blelham Tarn	Brown mud	*Scirpus* d, *Equisetum* a
67	Blelham Tarn	Brown mud	*Sparganium ramosum* d
68	Blelham Tarn	Peaty	*Phragmites* d, *Scirpus* f
69	Blelham Tarn	Peaty	*Scirpus* d, *Sparganium minimum* a
70	Blelham Tarn	Black, close	*Scirpus* = *Sparganium minimum*
71	Blelham Tarn	Black, close	*Sparganium* d

No.	Lake and depth (m.)	Type of mud	Vegetation
72	Blelham Tarn	Brown	*Phragmites* d, *Equisetum* f
73	Blelham Tarn	Brown	*Sparganium ramosum* d
74	Blelham Tarn	Peaty	*Phragmites* f, *C. elata* d
75	Blelham Tarn	Brown mud, III	*Scirpus* = *C. inflata* d, *Equisetum* f
76	Three Dubs Tarn	Peaty mud	*C. elata* d
77	Haweswater	Peaty mud	*Equisetum limosum* d
78	Blelham Tarn	Brown mud	*C. inflata* d
79	Blelham Tarn	Brown mud	*C. inflata*
80	Haweswater	Brown mud	*C. inflata*
81	Blelham Tarn	Brown mud, III	*C. inflata* d, *Phragmites* f
82	W., Pullwyke	Peaty mud, III	*C. inflata* d, *Equisetum* f
83	W., Pullwyke	Peaty mud	*Scirpus* d, *Equisetum* f
84	Three Dubs Tarn	Black mud	*Typha angustifolia* d
85	W., Pullwyke	Peaty mud, III	*Sparganium* r
86	Ullswater, 17	Brown silt	—
87	Ennerdale, 50	Coarse silt	—
88	Windermere, 50	Black, semi-liquid	—
89	Coniston, 8	Black, semi-liquid	—
90	Esthwaite, 12	Black, semi-liquid	—
91	Blelham Tarn, 9·5	Dark brown, flocculent	—
92	Blelham Tarn	Brown, peaty	Surface with *Phragmites* rhizome
93	Blelham Tarn	Dark silt	0·5 m. below 92
94	Blelham Tarn	Dark, clayey	1 m. below 92, rhizomes of *Equisetum*

APPENDIX IV

Oxidation-reduction potential of fresh muds

Sample no.	pH	E_h in volts	rH
7	6·64	+0·151	17·88
9	6·40	+0·172	18·73
16	5·44	−0·080	8·15
24	6·60	−0·098	9·80
26	6·24	−0·084	9·58
27	6·62	−0·108	9·53
33	6·50	−0·107	9·30
34	5·98	+0·072	14·44
35	5·77	+0·017	12·12
56	7·10	−0·033	13·06
57	5·84	+0·025	12·54
60	6·29	−0·038	11·27
61	6·80	+0·004	13·74
66	5·88	+0·092	14·94
67	5·98	−0·018	11·34
68	5·80	+0·120	15·75
69	5·94	−0·003	11·77
70	5·74	+0·004	11·62
71	7·08	+0·065	11·94
72	6·18	−0·045	13·91
73	5·93	+0·005	12·01
74	6·82	+0·287	22·46
75	5·70	+0·050	13·13
76	5·68	+0·120	15·51
78	5·58	+0·065	13·40
79	5·64	+0·196	18·03
81	5·80	−0·010	11·26
84	5·79	−0·060	9·51
86	6·08	+0·057	14·08
87	5·67	+0·050	13·07
88	6·56	−0·068	10·77
89	6·20	−0·022	11·64
90	6·48	−0·150	7·79
91	6·38	−0·086	9·79
92	5·92	+0·057	13·80
93	5·84	+0·077	14·34
94	5·76	+0·250	20·17

APPENDIX V

Exchangeable bases in the mud samples

No.	Organic content as % dry wt.	Exchangeable bases expressed in mg. per 100 g. of dry sample: Calcium	Magnesium	Iron	Manganese	Aluminium	Actual values multiplied by 1000: Ca/Humus	Fe/Humus
1	9·92	179	33·2	Tr.*	0	6·0	18·0	0·03
2	7·34	97	—	Tr.*	0	1·5	13·2	0·06
6	16·86	394	55·5	Tr.*	0	9·9	23·4	0·03
7	8·04	171	—	1	Tr.*	1·4	21·3	0·12
9	10·76	85	33·7	1	0	1·3	7·9	0·09
24	14·24	342	—	194	12	11·3	24·0	13·60
25	30·70	975	—	315	—	79·0	31·8	10·20
26	11·66	151	35·3	294	20	5·3	12·9	25·20
27	20·64	256	51·5	331	137	11·9	12·4	16·00
28	29·98	330	32·8	334	7	24·0	11·0	11·10
29	25·28	182	17·6	428	32	0·0	7·2	17·10
33	31·12	344	34·8	782	Tr.	2·5	11·0	25·10
34	27·32	389	48·0	38	0	0·0	14·2	1·40
35	26·34	245	25·6	272	2	1·4	9·3	10·30
58	5·76	218	—	44	9	4·1	37·8	7·70
59	25·08	—	—	2	—	56·9	—	0·10
62	23·52	231	—	240	145	1·3	9·8	10·20
81	55·64	430	52·7	182	37	2·1	7·7	3·30
82	36·68	653	21·8	42	Tr.	14·0	17·8	1·15
85	42·36	356	34·0	278	22	0·0	8·5	6·60
87	12·84	79	32·0	71	34	7·5	6·1	5·50
88	16·84	170	—	317	9	7·4	10·1	18·80
92	66·00	738	75·0	400	9	33·2	11·2	6·10
93	45·84	374	54·2	453	29	31·2	8·1	9·90

* Values negligible, 0·3–0·5 mg.

APPENDIX VI

Chemical analysis of plants

(Results of analysis expressed as percentage of dry weight)

Plant locality	*Chara fragilis* Congo Bay	*Chara fragilis* Derwent-water	*Nitella opaca* Low Wray Bay	*Littorella uniflora* Fisherty How	*Littorella uniflora* Pullwyke	*Isoetes lacustris* Fisherty How	*Isoetes lacustris* Low Wray
No. of mud sample ...	37	41	24	2	62	7	1
Total nitrogen	6·28	8·15	7·09	2·80	2·67	2·76	2·89
Ash	31·43	18·87	23·64	14·66	13·46	16·82	30·77
SiO_2	7·60	4·38	13·51	3·47	3·48	5·44	18·93
CaO	17·38	6·85	1·73	1·67	1·35	0·74	1·38
MgO	0·42	0·34	0·36	0·47	0·28	0·46	0·26
Fe_2O_3	1·56	1·38	0·85	0·29	1·13	0·39	1·03
Mn_3O_4	0·49	0·26	0·04	0·05	0·35	Tr.	0·33
Al_2O_3	1·56	0·92	1·79	1·37	0·93	2·30	2·42
PO_4	0·87	0·82	0·48	—	—	—	1·12
Crude protein	39·23	50·95	44·32	—	—	—	24·34
Ether extract	—	1·50	—	—	—	—	—
Crude fibre	—	11·46	13·92	—	—	—	16·51
Soluble carbohydrates	—	14·68	12·92	—	—	—	27·28

Plant locality	*Juncus fluitans* Derwentwater	*Sparganium minimum* Congo Bay	*Sparganium minimum* Pullwyke	*Sparganium minimum* Pullwyke	*Elodea canadensis* Pullwyke Bay	*Myriophyllum* Pullwyke Bay
No. of mud sample ...	15	39	35	85	40	—
Total nitrogen	4·16	5·87	5·00	3·28	7·72	5·99
Ash	23·33	18·07	26·92	21·65	20·77	21·19
SiO_2	16·62	6·71	10·87	3·63	4·20	11·48
CaO	0·91	2·10	2·78	1·23	2·18	3·15
MgO	0·06	0·25	0·41	0·47	0·23	0·11
Fe_2O_3	0·87	—	4·16	6·25	1·02	0·61
Mn_3O_4	0·02	0·26	0·04	0·19	0·10	0·11
Al_2O_3	1·85	0·84	1·09	2·00	1·43	1·36
PO_4	0·51	0·88	0·72	—	1·01	0·71
Crude protein	26·01	36·66	31·03	—	48·23	37·44
Crude fibre	15·92	11·37	11·58	—	15·84	16·63
Soluble carbohydrates	32·62	42·40	29·55	—	16·37	22·61

Plant locality	*Polygonum amphibium* White Cross Bay	*Potamogeton lacustris* Low Wray Bay	*Potamogeton lacustris* Pullwyke Bay	*Potamogeton obtusifolius* Pullwyke Bay	*Potamogeton perfoliatus* Fisherty How	*Potamogeton perfoliatus* Coniston
No. of mud sample ...	16	26	31	—	18	23
Total nitrogen	2·50	6·77	6·41	6·98	4·81	7·57
Ash	8·00	13·88	18·88	13·12	13·78	16·82
SiO_2	0·95	4·98	9·24	3·31	2·54	1·95
CaO	1·38	1·68	1·43	2·40	1·52	1·91
MgO	0·29	0·24	0·21	0·16	0·60	0·42
Fe_2O_3	0·28	2·43	2·74	1·78	0·29	0·44
Mn_3O_4	0·03	1·05	0·82	0·33	0·01	0·03
Al_2O_3	1·33	1·75	1·19	1·21	0·50	2·19
PO_4	—	0·03	0·09	0·18	0·43	1·14
Crude protein	—	42·31	40·10	43·64	30·04	47·30
Ether extract	—	—	—	—	1·60	—
Crude fibre	—	15·84	15·84	16·14	14·50	—
Soluble carbohydrates	—	26·47	24·33	25·60	40·08	—

Plant locality	*Potamogeton perfoliatus* Ullswater	*Potamogeton perfoliatus* Low Wray Bay	*Potamogeton perfoliatus* Pullwyke (shallow)	*Potamogeton perfoliatus* Pullwyke (deep)	*Potamogeton perfoliatus* Congo Bay	*Potamogeton heterophyllus* Low Wray
No. of mud sample ...	19	24	30	31	28	26
Total nitrogen	5·32	6·25	4·88	6·24	3·72	6·33
Ash	16·90	17·59	18·11	15·45	16·40	19·95
SiO_2	1·86	3·58	5·13	3·99	—	10·71
CaO	1·80	2·01	2·66	2·60	—	1·48
MgO	0·55	0·73	0·83	0·39	—	0·10
Fe_2O_3	0·11	0·46	0·88	1·74	—	0·85
Mn_3O_4	0·08	0·02	0·08	0·10	—	0·07
Al_2O_3	2·31	1·57	1·34	0·24	—	1·15
PO_4	1·19	0·71	0·72	0·54	—	1·01
Crude protein	33·24	39·08	30·52	38·92	—	—
Crude fibre	—	—	12·10	15·43	—	—
Soluble carbohydrates	—	—	37·67	28·60	—	—

Plant locality	*Potamogeton praelongus* Congo Bay	*Potamogeton zizii* Coniston	*Potamogeton alpinus* Pullwyke	*Potamogeton alpinus* Pullwyke	*Potamogeton natans* Pullwyke	*Potamogeton natans* (leaves only) Congo Bay	*Nymphaea alba* (rhizome) Pullwyke
No. of mud sample ...	25	23	35	—	46	—	—
Total nitrogen	6·62	2·57	4·74	3·12	2·35	4·71	2·10
Ash	23·62	12·88	27·49	20·46	8·00	9·24	11·94
SiO_2	4·67	1·91	11·21	8·02	1·38	1·34	1·53
CaO	3·01	2·20	1·49	1·42	1·16	2·94	0·51
MgO	0·23	0·58	0·15	0·24	0·57	0·37	0·28
Fe_2O_3	0·45	0·13	6·20	3·99	0·28	0·09	0·27
Mn_3O_4	0·05	0·62	—	0·10	0·04	0·12	0·03
Al_2O_3	1·52	1·58	1·72	2·11	0·97	0·91	1·05
PO_4	1·15	—	0·39	—	—	0·28	—
Crude protein	41·39	—	29·63	—	—	29·44	—
Crude fibre	22·65	—	13·29	—	—	25·54	—
Soluble carbohydrates	10·84	—	28·09	—	—	43·51	—

Plant locality	*Nymphaea alba* (leaves) Pullwyke	*Nuphar lutea* (rhizome) Congo Bay	*Nuphar lutea* (leaves) Congo Bay	*Phragmites communis* (rhizome) Pullwyke	*Phragmites communis* (shoot) Pullwyke	*Scirpus lacustris* (rhizome) Pullwyke	*Scirpus lacustris* (shoot) Pullwyke
No. of mud sample ...	—	38	38	59	59	83	83
Total nitrogen	1·90	0·80	3·06	1·15	2·58	1·53	1·85
Ash	11·20	5·30	11·49	9·66	4·91	13·12	4·38
SiO_2	1·00	1·13	0·85	5·51	2·84	7·40	1·26
CaO	1·04	0·27	1·79	0·19	0·15	0·17	0·16
MgO	0·26	0·04	0·95	—	—	0·12	0·14
Fe_2O_3	0·04	0·17	0·08	0·14	0·01	2·43	0·04
Mn_3O_4	Tr.	0·03	0·04	0·02	0·03	0·40	0·15
Al_2O_3	1·10	0·97	1·13	0·91	0·53	0·81	0·96

Plant locality	*Equisetum limosum* (rhizome) Pullwyke	*Equisetum limosum* (shoot) Pullwyke	*Carex elata* (rhizome) Pullwyke	*Carex elata* (shoot) Pullwyke	*Calamogrostis lanceolata* (rhizome) Pullwyke	*Calamogrostis lanceolata* (shoot) Pullwyke
No. of mud sample...	62	62	82	82	—	—
Total nitrogen	1·05	1·81	1·18	1·14	0·91	1·56
Ash	9·93	12·09	8·67	3·82	4·96	4·74
SiO_2	1·11	4·40	4·38	1·28	2·43	2·75
CaO	0·88	1·23	—	—	0·12	0·10
MgO	0·09	—	0·19	0·11	0·04	0·14
Fe_2O_3	4·18	0·10	2·71	0·07	0·57	0·01
Mn_3O_4	0·27	0·13	0·02	Tr.	0·08	0·01
Al_2O_3	2·93	1·08	—	0·60	0·26	0·46

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LIFE FORMS OF PASTURE PLANTS IN RELATION TO TREADING

By G. H. BATES

(*With Plate VII*)

THE structural adaptation of certain pasture plants to resist the injury of treading was stressed in a recent article by the author (1935). It was suggested that the property was possessed by virtue of their life form and that the plant community of a footpath, formed by human agency, composed in the main a synusia of cryptophytes. Owing to pressure of space the writer was requested to omit statistical details and to summarize all data. This was, however, given in a previous article and a detailed comparison made with the surrounds of the path (Bates, 1930).

The subject has been approached again (Davies, 1938) with somewhat different findings. The following notes constitute an attempt to clarify the matter, as it is thought that the second writer has drawn conclusions from habitats of a different nature. In the first investigation examples were taken of footpaths trodden by the human foot and *Poa pratensis* was found to be a constant member of the community. It occurred in zones often sharply demarcated, parallel with the axis of the path and adjoining the central portion, which is usually devoid of vegetation. Davies, in his survey, records *P. annua* as occupying the more severely disturbed zone, and this is the main point in which the two accounts would appear to be at variance.

It must be pointed out that he has considered grass verges adjoining carriage ways and also sheep and cattle tracks as being comparable with footpaths produced by human treading. In a later publication (Bates, 1937) marginal regions of the wayside have been placed in a separate category to footpaths, in the belief that they owe their characteristic vegetation to different sets of mechanical influences.

It must be agreed that there is a great variation in the component species of these habitats, as distinct from footpaths, presumably owing to the variety of forces at work. *P. annua* has been found in the majority of examples and at certain seasons it may be dominant in unstable zones, such as in shifting mud. It is characteristic of habitats where the earth is deeply disturbed and moved by wheels of vehicles, scavenging operations or hoof pressure. On the other hand *P. pratensis* is found in any stable turf at the wayside where it is trodden on the surface by human feet. Numerous examples may be observed close at hand, and it is worthy of note that in the only footpath, from which livestock was excluded, described by Davies (Table VIII, col. II, p. 47) *P. pratensis* occurs in measurable amount. *P. annua*, in this case, occupies a position of much less importance than in his other analyses.

There is no possibility that the species described as *P. pratensis* can be an ecotype of *P. annua*, for the identification has abundant confirmatory support. It is difficult to agree with the suggestion that *P. annua* cannot be regarded as a true therophyte, because it may become stoloniferous and perennial in certain habitats. The same phenomenon may occur in the case of a number of species of plants subjected to defloration and other interference with their normal cycle.

The effect of the human foot may be demonstrated to be different to that of animal hooves or the wheels of vehicles. It has been stressed in another paper (Bates, 1936) that, apart from compression, there is the rotatory twist of the sole and, owing to the flatness and comparatively greater area of the foot in proportion to body weight, the action is a surface one when the turf is stable. A "grinding in" effect results as well as that of bruising, but it is difficult to see how this movement or the process of puddling can bring about "aeration" of the soil. This latter term as well as that of compression is used too loosely in connexion with agricultural practices.

There is no visible rotatory twist in the feet of cattle, sheep or horses; their progression is digitigrade and they are quadrupeds. A much greater weight is carried per unit of area by the feet of animals, and their surface is not flat. A rotatory twist coupled with compression is a type of mechanical force which has not had the consideration it deserves, and its reproduction for certain cultural practices might be exploited to advantage.

It may be asserted that for the above reasons sheep tracks cannot be compared to footpaths. The formation of the latter is always a gradual process, but the former may appear upon a pasture within a few days of the introduction of a flock. Gateways appear to have been considered by Davies only in respect of their gramineous flora. The zonation of their vegetation has, however, been investigated in detail in relation to varying degrees of disturbance (Bates, 1936).

There is an abundance of therophytes characteristic of this habitat and *Plantago major* is usually a constant. In the region between the gateposts, when during wet winter weather the ground is severely disturbed by the hooves of animals and by wheels, there is a growth of annuals, resistant to treading during summer while the surface is stable. These consist of *Polygonum aviculare*, *Matricaria suaveolens*, *Senebiera Coronopus* and maiden plants of *Plantago major*. During winter the latter are squeezed out or buried in the mud and are established only in the outer zone where there is less severe seasonal disturbance. *Poa annua* will occur scattered all over this area especially in temporarily undisturbed parts (see Bates, 1935). At the ecotone *Lolium perenne*, *Poa pratensis* and *Trifolium repens* are present, except in arable fields. Gateways provide an excellent example of the selective action of varying degrees of disturbance, from deep puddling to surface bruising, upon the plant community.

Taking the species *Poa pratensis*, *Lolium perenne* and *Trifolium repens* as the dominant components of the footpath vegetation, their cryptophytic life form may be convincingly demonstrated by cutting sections of turf at right angles to the axis of the footpath, and extending out into the surrounds.

The fact that the above species are capable of recovery from the injury of treading as compared with *Agrostis* spp., *Festuca ovina*, *Holcus* spp. or *Agropyron repens* is well established. Direct experiment demonstrated the actual processes (Bates, 1935, pp. 478–9); see photographs, Pl. VII.

A question under discussion is whether increased fertility in the trodden zones or earthing up of the soil against the plants is not also responsible. It is rarely possible to find the typical footpath community upon dry sandy heaths, and this has been ascribed to the absence of puddling on the surface and a proper grinding of the vegetation. It is of course possible that there may be a level of fertility below which the species cannot grow. The influence of manuring by the grazing animal, however, can be discounted, for typical footpath communities are found in areas from which it is completely excluded. Earthing up by soil pressed to the sides of the path has been mentioned, but many examples may be found where, owing to slope, the mud is pressed away from the grass. In any case a cryptophyte possesses the life form most likely to withstand burying by puddled earth.

In an earlier investigation importance was attached to the fact that the dominant grasses of the footpath possess a conduplicate structure of the leaf and stem as compared with species which do not withstand treading. In addition they may adopt the rosette habit of growth. Both these factors may contribute to their resistance to pressure. On the other hand *Poa trivialis* has a conduplicate leaf arrangement without being a cryptophyte. It is not found as a component of the footpath community, and it would thus appear that life form is of primary importance.

Acknowledgements

My thanks are due to Dr W. B. Turrill and Mr C. E. Hubbard of Kew and to Mr S. F. Armstrong of the National Institute of Agricultural Botany, who identified specimens from the trodden zone of the footpath as *Poa pratensis*. Mr Armstrong confirms the observation that *P. pratensis* is characteristic of the stable trodden zone, and *P. annua* of the unstable and shifting.

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Phot. 1. Rows of plants before treading on. From the left to the right the rows are of: *Trifolium repens*, *Dactylis glomerata*, *Poa pratensis*, *Lolium perenne*, *Festuca pratensis*, *Agrostis stolonifera*, *Agropyron repens*, and *Trifolium repens*.

Phot. 2. Footpath trodden through the rows of grasses and clover. All have recovered after a resting period, except *Agrostis* and *Agropyron*, both dead and bleached in appearance. From the rear forward, the species are *Trifolium repens*, *Dactylis glomerata*, *Poa pratensis*, *Lolium perenne*, *Festuca pratensis*, *Agrostis stolonifera*, *Agropyron repens* and (in foreground) *Trifolium repens*.

BATES—LIFE FORMS OF PASTURE PLANTS IN RELATION TO TREADING

DISTRIBUTION OF WEED SPECIES ON ARABLE LAND

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(*With nine Figures in the Text*)

Introduction

Statistical methods usually give more precise information and definite knowledge, and are, therefore, coming to be widely used in analytical studies of plant communities. Their application has, however, been restricted to the studies on the distribution of individual species. Thus, the nature of distribution of individuals of the different species in communities of natural plant formations is now known, but the exact mode of distribution of weed species on arable land remains little understood.

In a previous paper (Singh & Chalam, 1937), a study was made of the distribution of certain weed species on cultivated fields which were returning to natural conditions on being left fallow for one or two seasons, thus allowing the chance factor to operate through the stages of natural plant succession. It was then shown that the nature of distribution of weed species on arable land was dependent on the mean density and the mode of reproduction. Individuals with high mean density and vegetative modes of reproduction are not distributed at random.

But leaving the lands fallow for more than one season is not generally practised, and even when they are left as such for a short time, various weeds, both annuals and perennials, crop up. A knowledge of the distribution of the various weed species under such conditions is thus necessary, and is likely to aid in analysing the causal relation between weed distribution and the environmental and other factors, or in the correlation of the increase or decrease of some species with the change of cultural practice or the use of manures and fertilizers, thereby facilitating the planning of crop rotation or the adoption of other methods of weed control. The investigations reported here are therefore designed and undertaken primarily to studying the distribution of weed flora on arable land when the fields are left fallow for a relatively short duration.

In natural plant formations, the distribution of individuals of plant species varies widely. Studying the distribution of plant species on grassland communities, Blackman (1935) observes that only five species, the individuals of which could easily be counted, as propagation appeared entirely by seeds and consequently where the distribution could be compared with the terms of Poisson series, showed random distribution over small areas. In other cases the distribution was markedly asymmetrical.

Comparison with the terms of Poisson series by estimating the significance with the χ^2 test serves as a good test of homogeneity but gives no measure of the degree of heterogeneity in the distribution of individual species. To measure the degree of dispersion of individuals, Ashby (1935) employs a new technique wherein he calculates the expected empty squares for each value of density. The correction factor applied to the equation measures the degree of heterogeneity. By employing this new method in a critical quantitative analysis of vegetation, he concludes that in a simple plant population under an almost uniform environment individuals of *Salicornia europea* show almost a random distribution, though there is but slight and significant under-dispersion.[1]

Clapham (1936) estimates the degree of departure from the Poisson distribution by relative variance (v/m). Using this method in a statistical study of some data of Steiger (1930) on the distribution of some prairie plants, he shows that the statistical units ("individuals") are not distributed at random in a great majority of cases but show "over-dispersion" (aggregation).

The degree of heterogeneity in the distribution of individuals can therefore be measured by both methods. Clapham's method of measuring the degree of departure from the Poisson series distribution is less laborious than the one suggested by Ashby, but as yet no comparison has been made of the estimates given by these two methods. The present investigations are therefore extended to estimate the heterogeneity in the distribution of the individuals of the weed species and also to compare the deviations from the random distribution when measured by both these methods.

Experimental results

Collection of field data

Counts of individuals were made towards the end of *Kharif*[2] season in September in five small plots that were left fallow from the end of *Rabi*[2] and throughout the whole of *Kharif* season (i.e. from April to September). All the plots had the same cultural history during the few preceding seasons. The samples were laid at random over all the plots which were quite far apart on the experimental farm. Sampling was carried out by means of a 6×6 in. quadrat. Such a quadrat was selected because of the extensive use to which it has been put in pasture research problems. 100 samples were taken from each plot.

For convenience of collection and computation of data for the purpose of analysis, collection of data was restricted to the counts of individuals only.

[1] The terms over- and under-dispersion are used often in two opposite senses. Ashby's interpretation appears to be more logical; the two terms are used here in the Ashbian sense. Thus over-dispersion means that the individuals are spaced farther apart while under-dispersion indicates aggregation of the individuals.

[2] *Kharif* means the monsoon crop season beginning from early July and continuing to September, while *Rabi* means the winter crop season from October to March.

Species where tiller counts or percentage area covered were obligatory were neglected because of the difficulty both in the collection and analysis of data. Further, such data bear no predictable relation to the actual density.

Distribution curves

Since in the present investigation the individuals of separate species are counted, the simplest assumption of chance distribution of their individuals has been made. The assumption in this type of distribution is that the chance that an individual shall occur in a given quadrat is the same for all the quadrats and is therefore independent of the position of the other individuals of the species. The values of the frequency occurrence in the different classes are given by the terms of the Poisson series:

$$e^{-m},\ me^{-m},\ (m^2/2!)\ e^{-m},\ \ldots,\ (m^x/x!)\ e^{-m},$$

where m is the mean frequency occurrence in the sample, i.e. the density of the species per sample. Thus e^{-m} will be the proportional number of samples containing no individuals, me^{-m} is the number of times one individual is present, and so on. The observed field data along with the estimations of the expected frequencies of quadrats with "n" occurrences are presented in Table I and representative species have been shown in Figs. 1–7.

In order to test the agreement of these curves with the expected Poisson type, the χ^2 test (Fisher, 1934) has been applied to find whether the discrepancies are to be taken as indicating a real divergence from the chance distribution or as sampling errors. The χ^2 test shows that amongst all the species where the frequencies have been compared with the terms of Poisson series, P is greater than 0·05 in thirteen species, e.g. *Bonnaya brachiata*, *Euphorbia erecta*, *Justicia diffusa*, etc., indicating thereby that the divergence is only due to sampling errors. Accordingly, it has to be inferred that the individuals of these species are distributed more or less at random and are neither markedly correlated nor spaced farther apart.

But in the other eight species, e.g. *Bonnaya veronicaefolia*, *Euphorbia hirta*, *E. thymifolia*, etc. (Table I), the χ^2 test shows that the odds against Poisson distribution is great and therefore the assumption of chance distribution is untenable. These species are either aggregated together or are spaced farther apart.

For those species where the odds against Poisson distribution are great ($P < 0{\cdot}05$), the discrepancy of the observed and calculated frequencies depends on the excess or paucity of the number of observed quadrats with certain occurrences, while a corresponding paucity or excess of the number of quadrats containing the same occurrences is exhibited in the calculated frequency classes. With zero or higher occurrences (four or five) per quadrat there is a greater number of quadrats in the observed series than in the calculated frequency classes, while in the intermediate classes the distribution of individuals is very

Table I. *Frequency distribution of weeds with "n" occurrences and the mean, the χ^2 test and probability and the relative variance of the various species*

	Frequency of quadrats with "n" occurrences																	Test		
	0		1		2		3		4		5		6		7					v/m
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Mean	Value	P	(obs.)
B. brachiata	42	39·01	86	79·58	70	81·17	50	55·18	30	28·15	16	14·46	6	4·91	0	1·32	2·040	3·060	0·80	1·040
E. erecta	52	50·16	33	34·61	11	10·16	2	2·75	2	0·48	—	—	—	—	—	—	0·690	0·168	0·90	1·130
J. diffusa	50	46·80	32	35·50	12	13·50	4	3·40	2	0·70	—	—	—	—	—	—	0·760	0·578	0·70	1·180
O. corymba	38	36·10	34	36·80	20	18·80	5	6·40	2	1·60	1	0·30	—	—	—	—	1·020	0·399	0·80	1·010
C. acutangulus	219	212·80	68	69·70	11	14·00	2	1·20	—	—	—	—	—	—	—	—	0·320	0·536	0·70	0·930
I. enneaphylla	243	232·90	48	53·60	6	6·20	3	0·50	—	—	—	—	—	—	—	—	0·230	1·812	0·50	1·500
L. nudicaulis	246	245·70	48	49·12	6	3·99	—	—	—	—	—	—	—	—	—	—	0·200	0·017	0·80	1·000
T. indicum	246	243·10	47	51·10	5	4·30	2	0·40	—	—	—	—	—	—	—	—	0·210	0·093	0·70	1·040
C. viscosa	264	266·10	31	31·90	5	1·90	—	—	—	—	—	—	—	—	—	—	0·136	0·160	0·50	1·200
P. quadrifida	267	266·10	29	31·90	4	1·90	—	—	—	—	—	—	—	—	—	—	0·120	0·020	0·80	1·100
A. aspera	270	267·50	25	30·20	5	1·70	—	—	—	—	—	—	—	—	—	—	0·116	0·152	0·50	1·100
G. pentaphylla	276	275·30	21	23·68	3	1·00	—	—	—	—	—	—	—	—	—	—	0·086	0·019	0·80	1·100
B. diffusa	279	277·00	18	22·20	3	0·90	—	—	—	—	—	—	—	—	—	—	0·080	0·204	0·50	1·100
B. veronicaefolia	98	89·50	94	108·50	69	65·60	26	26·90	10	8·00	3	1·90	0	0·40	—	—	1·210	3·509	0·40	1·216
E. hirta	96	90·31	101	108·30	58	65·00	36	26·01	8	7·80	1	1·89	—	—	—	—	1·200	5·355	0·20	0·983
A. baccifera	112	88·56	97	108·10	30	65·94	37	26·81	21	8·17	3	1·99	—	—	—	—	1·220	41·655	0·10	1·300
D. triflorum	129	111·10	91	107·70	55	52·30	20	16·90	5	4·10	—	—	—	—	—	—	0·970	6·370	0·05	0·907
E. thymifolia	42	36·10	30	36·80	16	18·76	8	6·38	4	1·60	0	0·33	—	—	—	—	1·020	4·088	0·20	1·150
P. Niruri	39	32·60	32	39·80	13	24·30	10	9·90	6	3·00	—	—	—	—	—	—	1·120	8·760	0·05	1·210
A. sessilis	249	241·70	39	52·34	10	5·64	2	0·40	—	—	—	—	—	—	—	—	0·216	1·158	0·20	1·180
V. cineria	255	244·90	37	44·10	6	4·00	2	0·30	—	—	—	—	—	—	—	—	0·180	0·653	0·30	1·200

N.B. All the above calculations are based on 100 average readings.

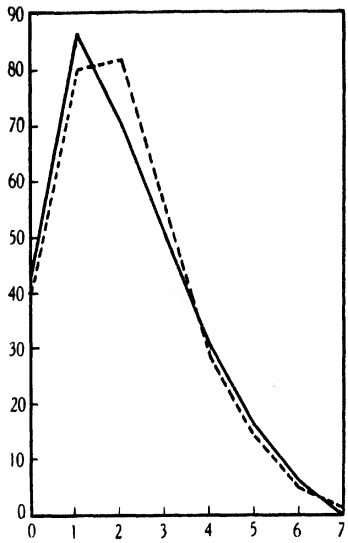


FIG. 1. *Bonnaya brachiata.*

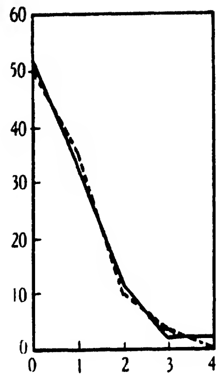


FIG. 2. *Euphorbia erecta.*

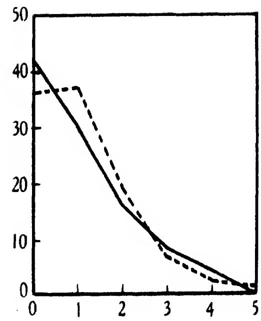
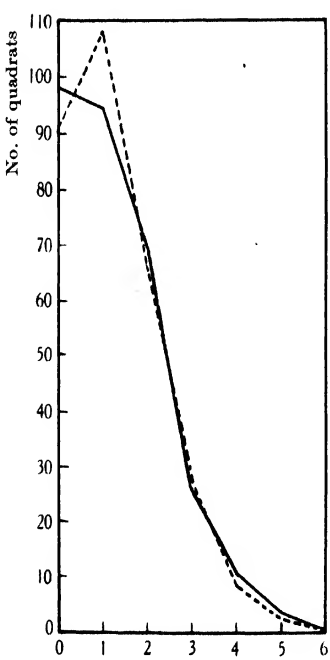
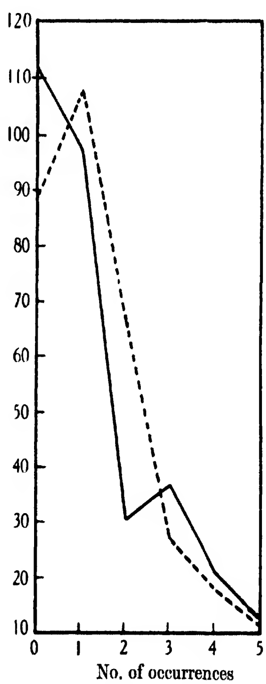
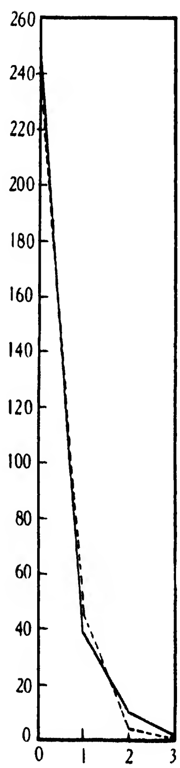


FIG. 3. *Euphorbia thymifolia.*







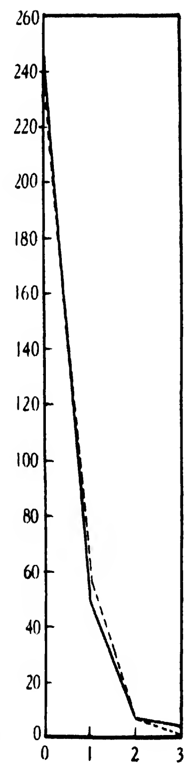


FIG. 4. *Bonnaya veronicaefolia.* FIG. 5. *Ammania baccifera.* FIG. 6. *Alternanthera sessilis.* FIG. 7. *Indigofera enneaphylla.*

FIGS. 1–7. Distribution curves of density for a few representative species. Continuous line indicates the observed frequencies, broken line represents the expected frequencies.

irregular. Species like *Euphorbia hirta* have an excess of observed number of quadrats with "2" occurrences while with other species the expected number is in excess with this occurrence. Other species like *Bonnaya veronicaefolia, Desmodium triflorum, Alternanthera sessilis* have an excess of observed number of quadrats with "3" occurrences while the reverse is the case with other species.

Relative variance

An important property of Poisson series is that the variance (v) is equal to the mean for all the values of m, so that v/m (relative variance) is always equal to unity. Taking advantage of this property, the relative variance (v/m) has been used as a measure of dispersion (Clapham, 1936). When the relative variance of a set of counts of individuals of a species is greater than unity, the dispersion of the individuals of the species will be greater than expected on the assumption of random distribution of the species (aggregation or under-dispersion). On the other hand, if the relative variance is less than unity, the dispersion is less than expected under the assumption of chance distribution, i.e. the individuals are spaced farther apart (over-dispersion).

When the relative variance of all the species are calculated from the formula

$$S_1^n \frac{(x-m)^2}{(n-1)\,m},$$

it is seen (Table 1) that with the exception of three species, viz. *Corchorus acutangulus, Euphorbia hirta,* and *Desmodium triflorum* where the relative variance in each case is less than unity, all the other species show a relative variance slightly greater than unity. *Launaea nudicaulis* is, however, the only species to give a relative variance which is exactly equal to unity.

It is therefore seen that in the majority of species, the relative variance becomes slightly greater than unity indicating thereby that most of the species show a tendency to be aggregated together. Only three species *Corchorus acutangulus, Euphorbia hirta* and *Desmodium triflorum* have a type of distribution where the species are spaced farther apart and therefore show antagonism. It is of interest to find that *Launaea nudicaulis* is the only species where the individuals should be distributed in good agreement with Poisson distribution. It is seen that the relative variance is slightly more than unity for species that appear to be distributed at random as indicated by the χ^2 test and also for those species where the hypothesis of chance distribution is disproved as P is less than 0·05. The divergence of the relative variance in the species *Bonnaya veronicaefolia, Euphorbia hirta,* and *Desmodium triflorum* is in good agreement with the Poisson series distribution, but the disparity of the results given by relative variance and the χ^2 test for Poisson series distribution in the majority of the species is most striking. From a theoretical consideration v/m must always be unity whenever the probability of fitting the observed frequencies with the calculated ones is equal to or greater than 0·05. The departure from

this expectation therefore suggests that either the relative variance or the comparison with Poisson series determinations does not indicate a true picture of the distribution of individuals.

But the divergence of relative variance from unity in all these cases is very small and hence it may be concluded that though these species show a more or less random distribution as indicated by the χ^2 test for comparing with the Poisson series, there is a tendency amongst them to be aggregated together. This may be explained by the limited range of dispersal of seeds and also the non-randomness of their dispersal.

Measurement of dispersion by Ashby's technique

It is of interest to compare the relative variance with Ashby's technique. In comparing the two methods for measuring the degree of dispersion, the species *Bonnaya brachiata* has been selected, since in the other part of the work this species has shown the highest mean density.

The experimental technique consisted in sampling the population with a quadrat of 50 cm. square divided into a lattice of 25 subsquares, each of 100 sq. cm. Observations were recorded on the total number of individuals in the quadrat and the number of empty squares. 100 such quadrats were selected at random in the same plots where the data for the earlier part of the work were recorded. Data on the total number of individuals in the quadrats and the percentage frequencies are recorded in Table II.

Table II. *Number of individuals (N.) of* Bonnaya brachiata *in quadrats of 2500 sq. cm. in area and the percentage frequencies (% F.) from squares of 100 sq. cm. in area, laid twenty-five times in each quadrat*

N.	% F.	N.	% F.	N.	% F.	N.	% F.
18	28	7	24	61	88	172	100
220	100	19	64	30	68	29	68
120	100	67	80	174	100	8	24
43	80	73	92	4	16	14	44
12	40	6	16	23	60	57	96
5	20	35	76	12	36	72	96
25	60	39	64	32	80	54	80
19	56	17	52	11	28	96	100
80	92	123	100	8	20	216	100
14	36	26	52	13	32	19	48
5	16	37	88	69	80	6	16
23	60	4	12	28	56	27	52
13	40	215	100	64	72	34	76
6	20	21	72	52	76	25	56
174	100	5	20	19	56	21	52
76	92	38	64	195	100	10	32
7	20	74	92	8	28	8	24
12	36	184	100	32	80	53	88
91	100	96	100	35	68	142	100
93	92	74	84	23	64	4	16
19	60	16	44	41	92	29	68
154	100	5	16	5	20	17	48
22	44	58	68	42	88	36	72
161	100	17	48	24	72	61	76
21	44	232	100	105	100	47	88

The basic idea of the method consists in concluding from theoretical grounds that if the relation between frequency and density is logarithmic, the distribution of the individuals is at random. Thus the values of density (individuals per sq. cm.) plotted against $\log_e q$, where q is the chance of not finding a plant

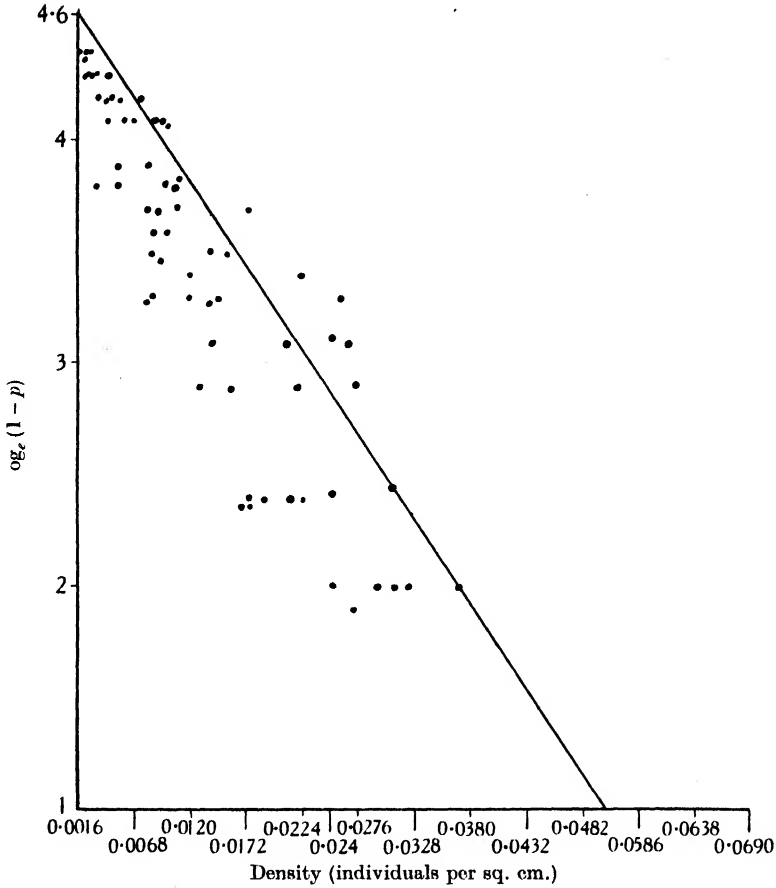


FIG. 8. Scatter diagram of the density of *Bonnaya brachiata* in individuals per sq. cm. plotted against the logarithm of chance of not finding any individual in a quadrat of 100 sq. cm. in area. Theoretical line on the assumption of random distribution is also shown.

in a quadrat, should fall along a straight line. Fig. 8, where density (individuals per sq. cm.) of *B. brachiata* is plotted against $\log_e (1-p)$, i.e. the logarithm of percentage absence of the individuals, shows that the points are scattered around the theoretical line calculated from the formula

$$x = \frac{-\log_e q}{k},$$

where x = the number of individuals per unit area and k = the quadrat size. It indicates therefore that the individuals of *B. brachiata* are distributed roughly at random.

Because it is very laborious to weigh each value according to its variance in order to test the agreement between the observed values and the theoretical line, such a test has not been applied. But Fisher and Stevens' (Ashby, 1935) sensitive test of random distribution is applied to test the hypothesis of chance distribution of the individuals of the species. The expected number of empty squares (squares with zero occurrence) in any sample quadrat for the particular density is given by the formula

$$E = n\left\{\frac{n-1}{n}\right\}^s,$$

where E = expected number of empty quadrats, n = total number of squares in the lattice (25 in this case), and s = the density, i.e. the number of individuals per quadrat. The variance of the observed number of empty squares for each quadrat is calculated from

$$V = n\left\{(n-1)\left(\frac{n-2}{n}\right)^s - n\left(\frac{n-1}{n}\right)^{2s} + \left(\frac{n-1}{n}\right)^s\right\}.$$

In Fig. 9 the number of empty quadrats is plotted against the corresponding density. The theoretical line is calculated from the above indicated equation. Since the points are grouped around the theoretical line, it therefore shows that the distribution of the individuals of *B. brachiata* is roughly at random. But, since most of the points lie above the theoretical line, it may be concluded that there are more empty quadrats than the theoretical assumption permits. Departure from random distribution has been tested by comparing the difference of observed and empty quadrats with the variance of the observations. Standard deviation and the difference indicate (Table III) that there is a very slight under-dispersion or aggregation among the individuals of the population.

Table III. *Test of significance of the observed and expected empty squares*

Sum of the number of empty squares				
Observed	Calculated	Difference	Sum of differential variance	σ
848	818·67	29·33	119·42	10·9

The departure from random distribution has been estimated by applying the following modified equation

$$E_{\text{calc.}} = n\left(\frac{n-1}{n}\right)^s \{1 - s(s-1)c\},$$

where c is the correction for heterogeneity, i.e. it measures the degree of heterogeneity. The fitted curve is shown by a dotted line in Fig. 9 and the value of c

for the quadrat size is $68{\cdot}38 \times 10^{-5}$. Thus it is observed that the individuals of *B. brachiata* show some degree of under-dispersion.

This conclusion is in agreement with the one obtained by the determination of the relative variance of this species. Thus although the comparison with the Poisson series distribution and the χ^2 test show that the chances are in favour of such a hypothesis, both the relative variance and Ashby's technique conclusively show that there is a slight aggregation among the individuals of the species.

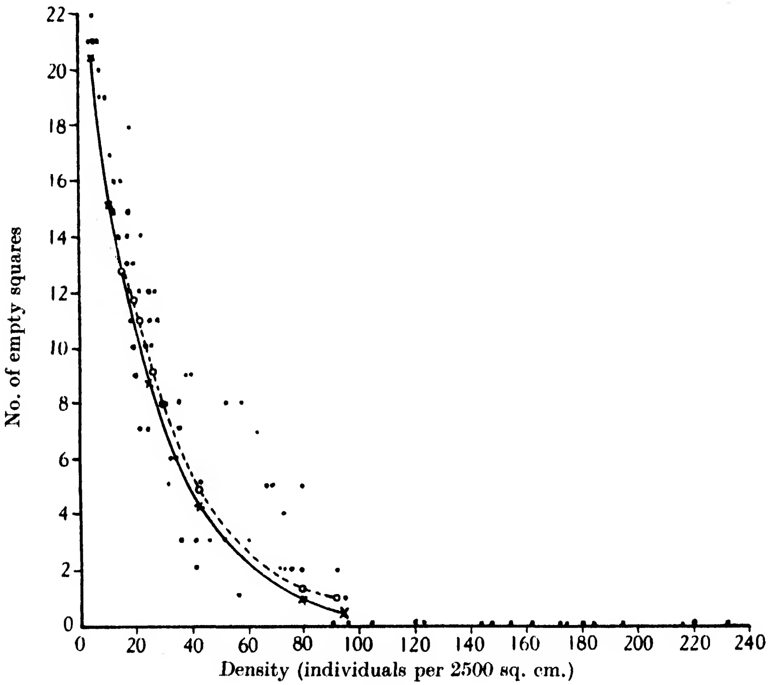


FIG. 9. Number of empty squares in quadrats plotted against density together with the theoretical lines. Continuous line is drawn without correction factor and the broken line with correction factor.

This determination further shows that there is a fair agreement between the results obtained by these methods.

DISCUSSION

From the above estimates it appears that even those species that show a good agreement with the terms of Poisson series and therefore of chance distribution show a slight degree of under-dispersion as indicated by the determination of relative variance. There appears to be, therefore, a disparity between the conclusions arrived at by relative variance and by comparing with

the calculated terms of Poisson series by the χ^2 test. The divergence from relative variance in all cases is, however, small and the deviation from random distribution is therefore correspondingly small. This is also corroborated by the determination made in the case of *B. brachiata* of the degree of the heterogeneity in the distribution of individuals by Ashby's technique of comparing the observed and empty squares for each of the values of the density contained in random quadrats.

This would suggest that although the homogeneity in the distribution of individuals of many species may be shown by comparing with the terms of Poisson series, there may still be a slight degree of heterogeneity detectable only by other methods. Thus in a study of plant population both the comparison with the terms of Poisson series and the calculation of relative variance have to be made if a knowledge of the exact mode of distribution of the individuals of different species is aimed at. Comparison with the terms of Poisson series gives a rough estimate, but relative variance or Ashby's modified formula with the correction factor brings more precise information.

The under-dispersion of individuals of the majority of these species appears to be dependent on the non-random distribution of seeds and their limited range of dispersal. Besides, some of the weed species may be reproduced by means other than seeds, which makes aggregation all the more possible. Other factors that may bring about such a type of distribution have to be sought in the characteristics of the environment or in the peculiarities of the weed species.

It has been shown previously (Singh & Chalam, 1937) that the distribution of weed species depends on the mean density and the mode of reproduction. In the present investigation, it is observed that the species where each individual[1] could be counted with ease show under-dispersion. It is therefore more likely that weed species reproduced vegetatively should show strong under-dispersion. This further suggests that when the individuals are counted separately, the mean density may not always bear a predictable relation with the type of distribution, although with vegetatively reproduced species, e.g. *Cyperus rotundus*, such a relation may be apparent. Besides, the characteristics of weed species are correlated with their density and thus may be reflected in the type of the distribution of their individuals.

When the methods of Clapham and Ashby for measuring the degree of heterogeneity in the distribution of individuals of plant species are considered, it appears that in field practice where rapid estimations have to be made relative variance is to be advocated. Although the collection of field data and their computation is laborious in Ashby's technique, the superiority and the advantage of the method lie in testing the significance of the apparent conclusion by appropriate statistical tests and in predicting the correction factor for each size of quadrat employed.

[1] The term individual has been used in its strict sense and means each rooted shoot.

Summary and conclusions

In a statistical study of the distribution of individuals of twenty-one weed species made in small plots of arable land which were left fallow for *a short duration*, it is observed, by comparing with Poisson series terms and applying χ^2 test, that with thirteen species the chances for random distribution are significant, while for the remaining eight species such a hypothesis is disproved.

Determination of the relative variance indicates, on the other hand, that all the species excluding *Corchorus acutangulus*, *Euphorbia hirta*, *Desmodium triflorum* and *Launaea nudicaulis* show a value which is slightly more than unity. The individuals of the majority of the species, therefore, are not distributed at random but show a small degree of aggregation.

Thus there is a disparity between the conclusions arrived at by the method of Poisson series determination with the use of χ^2 test and of the relative variance. It may be concluded, therefore, that Poisson series estimations cannot bring out small degrees of heterogeneity in the distribution of individuals. It is suggested that for studies on the nature of distribution of individuals both the comparison with the terms of Poisson series and the determination of relative variance have to be made.

This is corroborated by the determination of the degree of heterogeneity made on the distribution of individuals of one species *Bonnaya brachiata* by employing Ashby's new technique and modified formula of comparing the observed and calculated empty squares in quadrats laid at random. Thus there is a good agreement between the results obtained by either relative variance or Ashby's empty square technique. The former method is, however, more rapid and hence advantageous but the latter is more precise.

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CLIMATIC CLASSIFICATION FROM THE STANDPOINT OF EAST AFRICAN BIOLOGY

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CONTENTS

I. INTRODUCTION

MY interest in the subject is prompted by the fact that in collaboration with the British Museum (Natural History) I have been collecting material for a faunistic study of East African forest birds, their distribution, which under present conditions is essentially discontinuous, and their differentiation as related to degree of isolation. When water is the isolating medium, geographical distance is of first significance. But in evaluating the isolation of communities within a continent distance is of minor importance compared with the nature of the intervening country. That needs to be assessed in terms of climate, which delimits the biotic potentialities, and vegetation, which tends to express them.

For the individual plant or animal the "standard climate" (as measured in a meteorological screen) is altogether less important than the eco-climate, "the sum-total of meteorological factors within a habitat" (Uvarov, 1931) or the ecidio-climate, "the climate of nooks, grooves, leaf-surfaces and other small places" (Swynnerton, 1936). Of recent years the impact of this idea on field biologists has been so forcible that there is a tendency to depreciate unduly

investigation of the standard climate. As a corrective it will suffice to bear in mind that eco-climates are no more than modifications of the climate measured under standard conditions and that for defined habitats we are, given the standard climate, increasingly able to predict the eco-climates.[1]

I have supported the view (Moreau, 1935*a*) that the vegetational formation is the immediate determinant of the avifauna, although within the same formation a change in altitude, which implies a temperature gradient, may be accompanied by great avifaunal changes. The degree of isolation of bird population is, then, assessable primarily by unsuitability of intervening vegetation; but under modern conditions in East Africa the vegetation is subject to wholesale change through human intervention; so that for an evolutionary view of bird distribution and differentiation full emphasis must be laid on the ultimate control, which is the standard climate. (Even that may be modified by vegetational changes; but to what extent is controversial.) Moreover, the climate determines also in no small degree the nature of the soil. "The pedogenic processes are mainly governed by temperature and by the balance of rainfall and evaporation" (Robinson, 1936).

The biological or the soil surveyor should, then, be able to compare his findings with the climatic map. This, in East Africa, or indeed the tropics generally, he cannot do; the maps have yet to be constructed; and their prospects depend as much on the existence of a suitable system of classification as on the accumulation of routine data. Numerous systems have been suggested and applied, some of them to local studies elsewhere, others to the mapping of the climates of the world. Several of the papers concerned are prefaced by partial reviews of earlier work, the most comprehensive of them apparently that of de Philippis (1937). In this present review I deal particularly with the classifications that are relevant to the conditions of a mountainous country within a few degrees of the Equator. At the same time, in order to increase the general value of the bibliography, I have included in it, with an asterisk, a few references that I have not been able to consult either in original or in summary.

It would have been impossible to attempt this review without the assistance of the British Meteorological Office, who supplied a bibliography of recent work; of the Imperial Bureau of Soil Science, who have gone to much trouble to obtain literature and provide summaries; of the British East African Meteorological Service, especially for unpublished data; and of Mr C. Gillman, who has supplied literature and ideas. Several people interested in the subject from various points of view have been good enough to read the MS. of this review. For constructive criticism I am particularly indebted to Dr C. B. Williams, Rothamsted, Mr A. Walter, Director of the British East African Meteorological Service, and Mr G. Milne, Soil Chemist at Amani.

[1] Eco-climatic investigations in East Africa have been recorded especially by Kirkpatrick (1935), Moreau (1935) and Swynnerton (1936).

II. Some important physical characteristics of East Africa

For this review "East Africa" consists of Kenya, Tanganyika, Uganda and Zanzibar, below about 10,000 ft. I exclude the small areas above the timber-line, about the peculiar climates of which we know nothing except by inference and analogy from such sporadic data as those brought together by Klute (1920) and Scaëtta (1934).

Characteristics of East Africa that will do much to determine the trend of this discussion are the following:

(1) The relief is complicated: while a large proportion of the entire area lies between 1000 and 1500 m. above the sea, there are, in addition to the compact Kenya Highlands, many isolated masses and ranges rising to greater heights. Those which are the upraised edges of tilt-blocks, or associated with faulting, often on an immense scale, tend to be scarped or even precipitous, with correspondingly abrupt changes in conditions. The masses of volcanic origin, though usually reaching the greater heights, are more evenly and gently sloping.[1]

(2) Since the whole of East Africa is within 12° of the Equator the annual range of temperature in all localities is smaller than it is anywhere in the Sub-tropical or Temperate Zones. From the Tanganyika stations I have tested and the records given by Walter (1937) for Kenya I conclude that the mean of the coolest month differs from the mean of the hottest by not more than 6° C. anywhere in East Africa up to about 2000 m., which compares with 12° at Lisbon, 15° at Nantes, 19° at Basel (Kendrew, 1927). And in East Africa even the difference between the mean maximum of the hottest month and the mean minimum of the coldest reaches 20° C. at only very few stations; on the coast this difference is barely 12° C. On the other hand the mean daily range is comparatively high, from 11 to 17° C. in the Kenya Highlands (Walter, 1937).

(3) In no month, and indeed probably on no day in the year, anywhere in East Africa (as defined) is the temperature such as to inhibit most biological processes, given moisture. Night minima, which depend so greatly on local cold-air drainage, do not anywhere under standard screen conditions regularly fall so low as zero in any month of the year.

(4) Annual variability in the temperature at the same station is so small as to appear insignificant, a characteristic of the Tropics generally. In those stations I have tested it does not exceed 1° C. in the mean maxima of the hottest month or the mean minima of the coldest.

(5) Over by far the greater part of East Africa rainless periods are well-marked, if not severe. In a prolonged drought the vegetation, with the exception of the succulents, which are nowhere in the majority, withers, sheds its leaves and ceases to transpire. (The importance of transpiration for soil

[1] While a map accompanying this paper would certainly help to make the discussion intelligible, it could hardly equal the coloured physical map of East Africa available in any good atlas; and it is to that I would refer the reader.

moisture may be inferred from the statement by Henrici (1937) that in the South African summer, grasses have an average daily output of 7–8 lb. of water to one pound of grass, bushes 3–4 lb. to one pound of leaves.) There is, in fact, evidence that the soil, especially where it is "heavy" and cracks deeply, soon ceases to lose moisture. A relatively stable condition of soil moisture and of vegetation is generally reached long before the end of the dry season. At Mpwapwa (in Tanganyika), which regularly experiences a dry season of 6 months, the soil under deciduous thicket loses most of its moisture within 4 weeks of the end of the rains (Staples, 1935, and personal communication). This result is comparable with that obtained experimentally in Mauritius by Walter (1922). Therefore during the subsequent dormant months the intensity of the desiccating factors, which may actually increase, is relatively without significance.

(6) The rainfall is determined to a high degree by (*a*) proximity to large bodies of water, (*b*) local relief, which is complicated, (*c*) aspect.

Examples:

(*a*) Rainfall at Mombasa 1170 mm.; at Mazeras, 12 miles inland, 980 mm.; at Mariakani, 20 miles inland, 795 mm.; all in the coastal plain below 200 m. (B.E.A.M.S. "normals", 1935.)

(*b*) Rainfall average 1929–36 at Kwamkoro Estate, alt. 1000 m. in the East Usambara Mountains, 2125 mm.; at Mnyussi, 7 miles away, alt. 300 m., at their southern foot, 1202 mm. (Kwamkoro records by East African Agricultural Research Station; Mnyussi records by Freiherr von Geldern-Grispendorf.)

(*c*) Rainfall average 1930–6 at Engare Narok, alt. about 1800 m., on the south of Mt. Meru, 1675 mm.; at Engare Olmotonyi, 5 miles away, with a southwest aspect and at 1600 m., 880 mm. (Records by Tanganyika Forest Department.)

Conditions are in fact very different from those in the favourite fields of climatic study, Australia and the United States east of the Rockies, where there is little to "interrupt the simplicity of the climatic pattern" (Kendall, 1935). It follows that East African rainfall cannot be represented organically except on a contoured map.

Neither the classification and mapping of the climates of East Africa nor organic representation of the rainfall have yet been seriously attempted. Even straightforward isohyetal maps making the best use of all published data are not available for the whole area, although they are in preparation by the B.E.A.M.S.[1]

[1] A useful popular account of the climate has been given by Walter & Grinsted (1935–6), and a much fuller account provided by Walter (1938*a*). The only attempt at comprehensive climatic mapping of East Africa with which I am acquainted is that of Kendrew (1927; retained in 1937 edition). His divisions are purely empirical and the result has grave defects, to some extent inseparable from the small scale. For example, his division 7, "the mountains with heavy rainfall", small and discontinuous areas in fact, makes a most misleading appearance. And under division 3,

III. Classifications of climate

A. *Classification by the Köppen system and derivatives*

Köppen's system (1918; finally restated 1936), evolved as a result of many years' vegetational researches, was the first in which temperature, rainfall and rainfall distribution were all used as criteria and his system has attracted much attention. The general consensus of opinion is that it is good as an ideal world-wide system, but not so satisfactory for more particular regional studies.

Of the five classes into which he divided the climates of the world, three occur in East Africa, namely:

A. Tropical rain climates: coldest monthly mean above 18° C.; rainfall (r cm.)-temperature (t° C.) relations as follow:

Rain through the year, r greater than $2t+14$.

Rainy season in winter, r greater than $2t$.

Rainy season in summer, r greater than $2t+28$.

This formula has been reconsidered again and again by Köppen (1922, 1928, 1936).

B. Dry climates. No temperature limitations, but rainfall-temperature ratios below the thresholds specified for *A* climates.

C. Temperate rain climates; mean of coldest month between +18 and −3° C. Rainfall-temperature ratios as in *A* climates.

These classes Köppen subdivided as follows:

Af. Hot damp forest climate. Always humid; driest month with at least 60 mm. rain.

Am. Forest climate, monsoon type. Moderate dry periods. At least 2 months with less than 6 rainy days.

Aw. Periodic dry savanna climate, with the following defined relationships:

Total annual rainfall (mm.) 1000, 1500, 2000, 2500.

Driest month at most (mm.) 60[1], 40, 20, 0.

the "middle plateau", are lumped such diverse areas as the populous agricultural land of Usukuma, Mkalama and Singida, and the uninhabited wastes east of Lake Rudolf (cf. Gillman, 1936; Baker, 1937).

The latest published rainfall map for the whole of East Africa is that incidental to Shantz & Marbut's (1918) map of Africa (1 : 25 million). Walter (1937) has published a map (1 : 2 million) of part of Kenya—a section of a draft for the whole of East Africa that he has kindly communicated to me—with certain temperature data as well as isohyets and insets showing the seasonal distribution of rainfall. The draft differs in important respects from three other isohyetal maps recently made; for Tanganyika by Sayers in 1932 and by Paap (1934); for Uganda by Thomas & Scott (1935). This last was compiled from the B.E.A.M.S. normals for 1933, the isohyets being drawn with the aid of local knowledge of the country (Thomas *in litt.*); the basis of Sayers' map is not now ascertainable; Paap's was constructed on the records for 1908 to 1913 ignoring all others and making an unwarrantable use of interpolation.

[1] The force of this definition is not apparent. A rainfall of 1000 mm. in the year, with at least 60 mm. in the driest month, i.e. at least 6% of the annual rainfall in each month of the year, is a well-distributed one, compared with the 2000 mm. and 2500 mm. rainfalls specified by Köppen as being in the same category.

BW. Desert climates. Rainfall-temperature ratio not exceeding half the threshold of *A* and *C* climates, i.e.

Rain through the year, r less than $t+7$.

Rainy season in winter, r less than t.

Rainy season in summer, r less than $t+14$.

BS. Steppe climates. Between *BW* and *A*.

Cw. Warm winter-dry climates: wettest month (in summer) with more than 10 times as much rain as the driest (in winter).

Cs. Warm summer-dry climates: wettest month in the winter with more than 3 times as much rain as the driest in the summer and that less than 40 mm.

Cf. Humid temperate climates with rain more evenly distributed than in *Cw* and *Cs*.

In his latest draft (1936) Köppen makes distinctions in the *C* climates, according to the season at which the rain falls, and others by temperature, including:

Ca. With warmest monthly mean above 22° and more than 4 months above 10°.

Cb. With warmest between 10 and 22° and more than 4 months above 10°.

g. Where the hottest month occurs before the summer solstice.

On this classification Köppen has provided two climatic maps of the world (1918, 1928) which in their incidental treatment of East Africa differ materially. I take the later, for a tracing of which I am indebted to the British Meteorological Office, as the definitive one from Köppen's point of view. For East Africa it is, however, in some respects inferior to the 1918 map, although on a larger scale. The chief features are that the Kenya Highlands and central northern Tanganyika appear as a *Cw* island; the south-west Highlands of Tanganyika and the Livingstones-Mahenge area as an extension of the great *Cwg* area of Northern Rhodesia. Practically all the rest of our area is *Aw*. This mapping obviously has grave defects: north-east Kenya, where agriculture is impossible, appears in the same category as the Kisumu-Jinja area (where a sugar industry flourishes without irrigation), the entire coast from Kismayu southwards, and the northern quarter of Tanganyika Territory. In part this is evidently due to the scale employed, but it appears also that Köppen has not done justice to his own classification.

This system of Köppen, discontinuous in nature as it is, has been widely adopted, e.g. by McDougall (1936), Russell (1931–2, 1934), Scaëtta (1933), Braak (*ca.* 1933), Gorczynski (1934), Kendall (1935), though numerous modifications have been suggested. McDougall's has few merits: he ignored Köppen's differentiation of summer, winter and well-distributed rainfall, and redivided Köppen's three wettest climatic classes on an arbitrary basis. Russell found a slight modification of the *BW*/*BS* boundary to accord better with the vegetational distribution of the U.S.A., and also preferred a different temperature boundary between certain cold climates that do not occur in

East Africa. Matthews (1931), on investigating the climates of Chile, found that there Koppen's formulae have "a practical significance", but only "owing to the virtual cancellation of the humidity factor by the wind factor, together with the influence of contrast in physiography".

Scaëtta set out to "enlarge and define" Köppen's classification for equatorial Central Africa by distinguishing, in addition to two high-altitude categories with which we are not concerned:

(*a*) *Forêt d'averse* between isohyets 1800 and 2400 mm. and isotherms 26 and 15° C.

(*b*) *Forêt de pluie fine* between isohyets 2400 and 1500 mm. and isotherms 14 and 7·8° C.

(*c*) *Forêt sèche d'altitude soumise au phenomène de foehn*, between isohyets 1000–1500 mm. and isotherms 19–22° C., and characterized by *Piptadenia Buchananii* and *Albizzia fastigiata*.

At least in Northern Tanganyika the *Piptadenia* occurs in such a diversity of climates that (*c*) is clearly a division applicable only to Ruanda; while (*a*) and (*b*) cannot be regarded as well-considered improvements to Köppen's classification. Scaëtta himself seems indeed to have preferred other subdivisions very shortly afterwards (1934).

Gorczynski's modification (1934) appears to affect only cold climates. Kendall (1935) made the criticism that seasonal concentration of rainfall is not defined. This point, one of cardinal importance, will be dealt with later.

Bowen (1932, 1933) is one of the few writers who have approached the problem of climatic classification from the point of view of a zoologist and the only one whose attention was confined to Africa. He evolved quite an elaborate system, with particular reference to avifaunal districts and based on the early efforts of Suppan (1896) and Köppen (1900). It is most remarkable that he does not seem to have referred to Köppen's later classification. In Bowen's work the stress throughout is on the number of months that average at least 4 in. of rain, not on the dry months. He also attaches much greater importance than Köppen to the statement of climate in terms of both maximum and minimum temperatures.

B. *Classification by functions of rainfall and evaporation*

Meyer (1926), simplifying earlier formulae of Szymkiewicz (1925), proposed the simple ratio of total rainfall to mean saturation deficit. Although this formula takes no account of certain factors, especially wind and the seasonal distribution of rainfall, Prescott (1934) after investigation concluded that in Australia "the Meyer ratio...appears to offer an efficient measure of rainfall-evaporation relationship" though it is "not quite perfect" (Prescott, 1937). Certainly it seems doubtful whether this ratio, calculated on a basis of annual

means, can give a satisfactory comparison of climates with drought periods of different duration. Jenny (1929) approved of the Meyer ratio as applied to United States data, but his investigation has been criticized with fatal effect by Crowther (1931).

Vazquez (1933) and Rosenkranz (1936) have put forward a "phyto-climatic index" and an "index of oceanicity" respectively, single values based on complicated formulae into which relative humidity is introduced as well as rainfall and mean and extreme temperatures. It is impossible to believe that such abstruse functions could have any general application.

The use of evaporation records from a free-water surface, or atmometer, have been advocated by Transeau (1915), Livingston (1916), Livingston & Shreve (1921) and Davidson (1934, 1935, 1936, 1937), who has mapped Australia on the basis of the precipitation-evaporation ratio. He calculated the saturation deficit for the 235 stations for which the necessary data of temperature and relative humidity were available; "interpreted these in terms of evaporation by reference to records for evaporation at the capital cities" of the Commonwealth states; and then classified the climates with reference to the number of months in which the evaporation bore a defined relation to the rainfall. Although the stations providing the data necessary for this calculation are perhaps not more geographically sparse in East Africa than in Australia, it is most unlikely that in the former area, with its fragmentary climatic pattern, the local reductions to evaporation could reliably be made. Moreover, as Gradmann (1932) has pointed out, in high altitude areas such as bulk large in East Africa, greater insolation, lower pressure and, locally, perhaps also greater air movement, tend to offset the effect of the lowered temperature that would reduce evaporation. The final stage in Davidson's classification is to designate temperature zones, his divisions being: "Hot", annual mean above 21° C.; "Warm Temperate", with mean of coldest month not less than 6° C. The latter figure is of no significance in East African conditions, but the former (21° C.) is the limit of the Tropical Zone in East Africa also (see VII).

C. *Classification by functions of rainfall and temperature*

Attractive as it may be to use a rainfall-evaporation ratio, the very general absence of the necessary data has demanded some alternative, and that put forward has usually been a function of rainfall and temperature. It will be noted that this was utilized incidentally in Köppen's system, though he did not, like the students named later in this subsection, make it his keystone.

To use temperature as an indicator of evaporation, ignoring those most important factors, wind and atmospheric humidity, may be admitted to be a last resort. Matthews (1931) indeed has described it as a "false assumption" that a relationship exists between mean annual temperature and evaporation loss. The method contains another weakness in that it involves using the minimum temperature, usually as a component of the mean. For the purpose

in view the recorded minimum is altogether less important than the dew-point. This seems to have been remarked only by Prescott (1934) and very briefly. A full recognition of this underlying fallacy stresses the empirical nature of all the formulae designed to evaluate precipitation efficiency that are mentioned in this subsection. The truth appears to be that any value involving the minimum temperature cannot have a physical basis or safely be used for comparing climates except within two distinct categories: (*a*) those with approximately the same dew-point, and (*b*) those so dry that no dew is deposited at all. In these dry climates, evaporation continues throughout the 24 hr. day. In more humid climates so long as dew is being deposited any function designed to evaluate rainfall efficiency must be inoperable, and for periods that will tend to vary with the dew-point, not necessarily with the minimum temperature reached. A time factor introduces itself, varying greatly in different types of climate and of differential importance.

Lang (1915) with his "rain factor", simply the annual precipitation (mm.) divided by the mean annual temperature (° C.), was perhaps the first to offer a formula based solely on these elements. His approach was that of a pedologist. A chief weakness of his formula, the inadequacy of which has been demonstrated, is its failure to take any account of the seasonal distribution of the rainfall. Stefanoff's scheme (1930) fails for the same reason—among others. The term "hygric continentality", obtained by dividing annual precipitation (mm.) by altitude (metres), is merely another and even cruder form of Lang's "rain factor", applicable only to localities having the same altitude-temperature relationships. Albert (1928) suggested a "reduced rain factor", derived from the rainfall and the mean temperature of the frost-free period only. The climates with which he was concerned have a single important character in common with those of East Africa, namely, a well-marked season when evaporation from vegetation and soil practically stops. McKibbin's attempt (1933) to deal with the same problem in Canada is not designed for general application.

De Martonne (1909) evolved first a climatic classification with a general resemblance to that of Köppen, but by no means so precise. Later, he formulated a classification of the drainage systems of the world in which the main heads were "areic" regions with no run-off, "endoreic", those of inland drainage in which streams run every year, however intermittently, and "exoreic", which drain into the seas. He then observed that each of these categories appeared to be connected with definite relations between rainfall and temperature. Finally he put forward (1926, 1926*a*, 1927, 1928) his "index of aridity", in effect a modification of the Lang rain factor, for it is obtained by the formula $\frac{P}{T+10}$, where P = the annual rainfall (mm.) and T the annual temperature (° C.). The index of aridity can be applied to the climate of single months or parts of a year by modifying the formula; for example, the index for

one month is $\frac{P' \times 12}{T' + 10}$, where P' = the month's rainfall and T' the mean temperature for the month. But by itself de Martonne's system does not admit of adequate weight being given to the duration of dry periods. It is unfortunate, as several authors have pointed out, that the higher the humidity of the climate, the higher de Martonne's index of aridity. Fenner (1930) suggested an arithmetical manipulation that would produce a more consistent-looking series of values; but his idea seems to have attracted no attention and is probably unnecessary.

According to de Martonne, indices below 5 on his scale denote true deserts (botanically); 5 to 10, dry steppes where agriculture without irrigation is impossible; 10 to 20 ±, prairies where "dry farming" can be practised. He added that at about 30 forest vegetation tends to predominate and at about 40 it gains complete control. De Martonne's threshold for "dry farming" is much too low for East Africa, where, so far as I can ascertain, no agricultural population maintains itself without irrigation under conditions more unfavourable than at Singida, Kondoa-Irangi and Mpwapwa, which have indices of aridity of about 20.[1] His threshold of 30 for forest is also on the low side; I doubt whether any East African forests exist under conditions more rigorous than those of the Olive and "Cedar" (*Juniperus*) communities of Mt. Meru and the West Usambaras, with indices of 33; and the rainfall those receive is supplemented by mountain mist (see V below).

A further elaboration of de Martonne's classification (1928) provides for "l'aréisme humide de plaine", defined as the regime under which rain-ponds (= "vleys") are formed but no drainage takes place, although the ground is temporarily wet. He is inclined to attribute this sort of "humid areism" to part of Tanganyika, specifying "the plateaux of Unyamwezi".

De Martonne (1926*a*, 1927, 1928) provided a world map of drainage categories which appears to be in the main satisfactory for East Africa; but his small-scale map (1926*a*) of indices of aridity is thoroughly bad for our area and not in accord with the application of his own formula to the published records. Incidentally, the formula tends to break down as T approaches 0° C., as pointed out by Perrin (1931) and others.

Perrin puts forward the index of 40 as the beginning of the optimum for forest, in approximate agreement with de Martonne's view, which has already been discussed. Perrin's other suggestion of the index of 20 as the minimum for ligneous formations cannot be accepted for East Africa without qualification. In acacia—desert-grass country the trees often grow so close together that it is not easy to pass between them, under an annual mean temperature of 25° C. and a rainfall of less than 500 mm.—even down to 370 mm., the six-year average at Garissa, in eastern Kenya, where the index of aridity is under 11.

[1] It is a remarkable fact that the 1908–13 averages given for these three stations by Paap (1934) are 523, 523, 616 respectively; the 8-year averages given in the B.E.A.M.S. "normals" for 1936 are 622, 689 and 657 mm.

De Martonne & Fayol (1935) have tried to improve the "index of aridity", while retaining simplicity of calculation in such a way that localities with marked seasonal rainfall could be more clearly differentiated from those where the rainfall is better distributed. After suggesting two formulae that are clearly unpractical, especially for East Africa, they are inclined to favour one in which the value used for comparative purposes is the mean of the annual index of aridity (calculated by the original formula) and the index of aridity of the driest month. This obviously cannot give anything like due weight to a long period (say four months) of practically complete drought.

Emberger (1930, 1932) has put forward a classification of "Mediterranean climates" which has been used by de Looze (1933) for mapping the climates of Katanga. Emberger suggested that the pluviometric factor should be taken as $\frac{P \times N}{365}$—a formula resembling Walter's (1910), referred to later—where P=rainfall (mm.) and N the number of rainy days; but he recognized that since N was often not available P would in many studies have to be used without correction. The important elements of temperature Emberger recognized as the mean maxima of the hottest month (M) and the mean minima of the coldest (m); and he pointed out that, generally speaking, in Mediterranean climates evaporation is nowhere high when $(M-m)$ is low. Hence for a single-value climatic factor where evaporation data are not available he evolved the pluviothermic formula $\frac{P}{2\left(\frac{M+m}{2}\right) \times (M-m)} \times 100$, i.e. $\frac{100\,P}{M^2-m^2}$, the $\frac{100}{2}$ being merely an arithmetical device to simplify the result. $\frac{M+m}{2}$ being always within a fraction of a degree equal to the "annual mean temperature" (as calculated in the usual way from the mean of the daily maximum and minimum), the new feature in Emberger's formula is the introduction of m into the expression twice. But since, as remarked at the beginning of this section, the low temperature significant from the point of view of evaporation is the dew-point, not the minimum, I regard the repeated introduction of m in calculating the quotient as an expedient of doubtful value; and in any case it must be less effective in East Africa, where the annual range of temperature is everywhere so low, than in the climates for which Emberger evolved his formula. His final classification of climates is obtained by plotting each with m on one ordinate and the pluviothermic quotient on the other.

Crowther (1931) from the pedological point of view proposed a classification by the "leaching factor", which was the number of centimetres of rainfall in the year minus $\frac{10}{3}$, the number of degrees centigrade denoting the annual mean temperature. The effect of this formula is to require an additional 3 mm. of rain for every rise of 1° C. in temperature, if the same leaching effect is to be maintained. This ignores the seasonal distribution of the rainfall, although, for

example, 500 mm. of rain concentrated in 4 months could hardly fail to have more leaching effect than 500 mm. spread evenly throughout the year. The data on which Crowther arrived at his formula are derived solely from Rothamsted lysimeters, on a single soil type and under the well-distributed rainfall of England.

Thornthwaite (1931, 1934) rejects both Köppen's and de Martonne's classifications, incidentally misquoting the latter's formula as $\frac{P}{T-10}$ instead of $\frac{P}{T+10}$. He offers instead a classification obtained by summing the individual months' "temperature efficiency" and "precipitation efficiency". Köppen (1936) has commented that a complicated evaluation of the former is unnecessary, a criticism that has especial force in East Africa, where the temperature always admits of most biological processes. Thornthwaite's "precipitation efficiency" is a complicated function of rainfall and temperature evolved to fit the evaporation data of 21 stations (with cold winters) in the western U.S.A. The complexity of the formula reduces the chances of their being adequately tested. Forbes (1932), however, found that the precipitation efficiency formula had to be modified even for eastern U.S.A. Jones and Bellaire (1937) think that Thornthwaite's classification, as modified by Forbes, is more satisfactory in Hawaii than Köppen's.

Thornthwaite (1933) has provided a world map of climates by his classification. In precipitation effectiveness no part of East Africa is adjudged to a lower category than "Sub-humid", under which practically the whole of India is also mapped; but in fact a great part of East Africa in the east and north of Kenya is a country of acacia—desert-grass or of desert scrub in which agriculture is impossible. Moreover Northern Tanganyika from 6° S., the south, east and north shores of Lake Victoria, the Kenya Highlands and the Northern Frontier Province up to above 6° N., heterogeneous as these areas are, Thornthwaite includes in the same subtype, *CB′ r*. This indicates "sub-humid, mesothermal, rainfall adequate at all seasons"; but in fact prolonged dry periods that cause agricultural operations to be strictly seasonal are characteristic of the greater part of the area.

D. *Classification by months with a defined climatic ratio*

Notwithstanding the defects of de Martonne's index of aridity, Andrews & Maze (1933) found it worked not unsuccessfully in Australia; but they broke new ground by classifying the climates there on the basis of the number of "dry months" in each year. These they defined as the months in which $\frac{\text{monthly rain (mm.)}}{T^\circ\,\text{C.}+10}$ does not exceed 1. The application of this to East Africa would mean that up to 1500 m. (5000 ft.), where the lowest monthly mean in any locality is at least 15° C., any month with less than 25 mm. of rain would

be "dry"; and, since the highest monthly mean anywhere in East Africa does not exceed 30° C., no month with more than 40 mm. of rain in any locality would rank as "dry".

The value accepted by Andrews and Maze as indicating a "dry" month agrees closely with that adopted by de Martonne. Scaëtta (1934) independently pointed out the importance of dry periods but his definition of these was wider, including all indices up to

$$\frac{12 \times \text{monthly rain}}{T+10}=20, \quad \text{i.e.} \quad \frac{\text{monthly rain}}{T+10}=1{\cdot}66.$$

At the same time he classified Ruanda on the basis of the number of months in which the precipitation is less than 50 mm. For Katanga a monthly precipitation of 20 mm. has been used as the upper limit for a "dry" month (De Looze, 1933).

Andrews and Maze find that in Australia the isoline of 8 dry months is highly significant: it coincides well with the limit of desert and semi-desert vegetation; it includes the area of endoreism; and it includes no area in which agriculture has been successful, though it comes close to the dry border of important wheatlands. Prescott (1934) agrees that this "method of enumerating those months of the year having some characteristic climatic ratio is of considerable promise".

A classification of, or by, dry periods on the lines of Andrews and Maze takes no account of the residual effects of rainfall, a subject referred to in Section VI. The evidence quoted in Section II (6) tends, however, to limit these effects to a short period after the end of the rainy season, although there can be no question that their duration varies greatly with the nature of both soil and vegetation. Köppen thought that the importance of a dry period varied inversely with the total annual rainfall. He mentioned that in Malabar, with a rainfall exceeding 2000 mm. annually, forest persists with a dry period of 4 months, whereas round Lagos, with 1500–2000 mm. of rain, 2 months dry period is a limiting factor. These statements need to be examined critically in the light of experience elsewhere: Chapin (1933) has stated that "in Sierra Leone, where there is a dry season of 4 months, a total annual rainfall of 170 in. (over 4000 mm.) does not suffice for continuous forest growth"; but in East Africa economically valuable mountain forest (*Juniperus procera* and *Olea Hochstetteri* communities) survives a dry season of four and five months on a total annual rainfall of barely 900 mm. (e.g. at Olmotonyi, Mt. Meru).

Davidson (1936, 1937) and Trumble (1937*a*) have both developed the method of Andrews and Maze, utilizing as their basis the ratio between precipitation and free-water evaporation, as explained in the previous summary of Davidson's work (III B). Davidson (1936) selects "$P/E=0{\cdot}5$ as the value below which adequate moisture will not be available for general plant growth at the soil surface, and in the upper layer of the soil". Trumble regards a value of P/E

greater than $\frac{1}{3}$ as necessary, under average conditions, for the surface of the soil to be maintained "at or above the wilting point".

Trumble's approach to the problem of these climates with definite dry seasons is opposite, or rather complementary, to that of Andrews and Maze and of Davidson. He defines a "period of influential rain", during which P/E remains greater than $\frac{1}{3}$. To utilize the length of this period in classifying East African climates has obvious attractions, but some alternative to the precipitation-evaporation ratio must be sought. It might be absolute monthly precipitation above a certain minimum; Williamson and Clarke (1931) regarded rainfall exceeding 1 in. in any month as effective in India; and in this connexion three independent estimates quoted by Davidson (1936) are of interest:

(*a*) "Only rains amounting to 0·20 in. do real good in an agricultural way" (New South Wales).

(*b*) "In the dry north of South Australia...an ecologically effective rainfall is one consisting of 0·15 in. or more and which falls during a distinct rainy period."

(*c*) In the same area in a dry period 0·25 in. is "nearer the minimum effective...; lighter falls do not penetrate the soil more than 2–3 cm."

From personal experience I am of opinion that for low altitudes in East Africa the estimates of 0·25 in. in (*c*) would be too low.

IV. Climatic variability

Climatic classification has always dealt in normals, and all the systems put forward have been based on them. But it cannot be too strongly emphasized that the abnormal is of great, and often of more than transitory, importance. In East Africa it is the dry years that favour the advance of pyrophytic savannah at the expense of evergreen forest, as has been stressed by Swynnerton (1917); and that is a process hardly reversible. In Section VI an instance is given of tsetse infiltration favoured by cloudiness, the results of which, at least in the absence of European organization, would be conclusive for cattle-keeping, and hence of great importance not only to human economy but to the vegetation. Variability is of even more obvious importance from the point of view of agriculture than from that of general biology. The farmer must have the right weather to germinate his seed at the right time, to enable the plant to grow, to yield many-fold at certain intervals and to ripen to time; failure of the weather to live up to expectations for two successive seasons may not merely scotch, but kill, a farming enterprise. On the other hand a natural plant population can survive if merely at some time or other during the life of the parent plants enough seed is produced to replace them. Natural herbaceous vegetation may, nevertheless, undergo great changes in consequence of variation in rainfall, even if the annual average total is maintained, as Henrici (1937) has described for the veldt of the Orange Free State. For these reasons, and

also because in East Africa the variability of annual and monthly temperatures is so limited, for the purpose of this discussion all the emphasis is to be laid on rainfall.

De Martonne (1926*a*) remarked that the boundary of areism is a zone rather than a line, a zone fluctuating from year to year with variations in climate. The idea has been greatly developed by Russell (1934). Using in the main Köppen's classification, he derives terms such as "desert year", "steppe year", "tropical year" and "tropical savannah year". Nuclear climatic zones are those in which all the years in the period fall into the same category. "Any region that normally experiences a recurrence of climatic years typical of nuclear climates on either side" is treated as transitional; and the boundary between nuclear climates can be indicated by the line through the points with 50 % of climatic years favouring each of the nuclear climates. Russell has been able to apply this "climatic year" fruitfully to the broad zonal climates of the United States of America. In East Africa, where the climatic pattern is so fragmentary, and moreover only the rainfall is effectively variable, an attempt to delineate nuclear and transitional climates could not be so successful.

The importance of rainfall variability has been recognized and its nature studied in several African countries, e.g. by Scaëtta (1934) in Ruanda, by Plummer (1926) and Wellington (1929) in South Africa, by Robertson (1927) in Rhodesia and by Maurer (1936) in South-west Africa. Robertson has remarked, with justice, that "a knowledge of the degree of variability of the rainfall of a particular locality is of almost more importance than a knowledge of the normal annual rainfall". The extent of the variation encountered in East Africa may be judged by the examples of Mombasa and Athi River where in the period 1905–35 the respective rainfalls varied from 830 to 1850 mm. and from 170 to 1040 mm. (Walter, 1937), and of Moshi, where only in the seven years 1927–33 the rainfall varied from 506 to 1742 mm. (Teale & Gillman, 1935).

The potential importance of rainfall variability is the greater if we accept the two generalizations to which Williamson & Clarke (1931) have given their support as a result of investigations in India, namely:

(*a*) The lower the average rainfall the higher the variability.

(*b*) Reliability is less, i.e. variability is greater, when rainfall is concentrated than when it is well distributed in time.

Wellington (1929) had already put forward the first of these generalizations so far as South Africa was concerned, but both require to be tested for East Africa. In an investigation based on the short and probably inadequate series of data then at his disposal, Kremer (1910) came to the conclusion that "the North East is exposed to the greatest variations" in Tanganyika Territory. For him the area consisted mainly of the stations at Tanga (on the coast), Amani (a rain-forest area) and Mombo (dry savannah). The first two have, for East Africa, exceptionally well-distributed rainfalls, and the second, Amani, an unusually high one as well. In a comparison of ten stations on and near

Kilimanjaro Teale & Gillman (1935) found that the one with the highest rainfall has the lowest variability, but it is by no means true that those with the lowest rainfall have the highest variability.

The necessity for a knowledge of variability being admitted, it is far from easy to decide on the method of evaluation. To start with, the idea of "normal rainfall", which underlies it, is delusive. It is the general practice to take for the "normal" the arithmetic mean. As Schumann & Thompson (1934) remarked it would be better to employ the term "floating average". Whether this is derived from all the existing records, or from a random sample of the existing records, or from all the records that fall within a selected period,[1] the result is liable to be distorted by the occurrence of one or more highly abnormal years. For this reason Chaptal (1936) urges the use of the median[2] instead of the mean rainfall as the "normal". Crowe (1936) has advocated the use of median and quartiles. The most abnormal years have to be taken into account once more in calculating the degrees of variability, and there is much divergence of opinion as to what weight they should be allowed. Napier Shaw (1936) says flatly: "I should regard extremes for any period as worth more... than means because the extremes represent the most potent features of experience in agriculture.... Smooth curves give no indication of the extremes which are of vital importance."

There has been much diversity of opinion about the method of evaluating rainfall variability. Plummer, Wellington, Robertson, Maurer and Crowe in the studies referred to above all used different ones. Paap (1934) produced two isohyetal maps of Tanganyika showing respectively the highest and the lowest rainfalls during his chosen five-year period—irrespective of whether the extremes in different localities fell in the same year.

Robertson's method (1927) is one of the most satisfactory. He took the arithmetic mean as the normal and the standard deviation as the measure of the variability. This gave the limits within which we may expect to find the annual rainfall for two-thirds of the years in any given period. He amplified this by expressing the greatest deviations recorded above and below the normal as functions of the standard deviation. These results, being expressed in percentages, permit of zones of equal variability, or, as he expresses it from the agricultural standpoint, of equal reliability, to be mapped. The biologist, however, is more concerned with the absolute deviations from the normal. Further, even allowing for the fact that the normal is only a floating average, it appears that outside rather narrow limits a variation below normal is much more likely to have important biological consequences than one of the same extent above. This is especially true of the agricultural consequences. "The

[1] The consensus of opinion seems to be (Conference of Empire Meteorologists, 1935) that the period should not be longer than 35 years nor shorter than 10; in East Africa there are few station series that exceed the higher figure.

[2] That value which is so related to those occurring in a given set of instances that exactly as many exceed as fall short of it.

scope and success of the farmer are largely limited by the variability of the rainfall, and especially by the amount and frequency of its minimum" (Gillman, 1938). Apart from the direct effect of the deficiency, Wilson & Savage (1936) concluded for Ohio that "evaporation increases with a decrease in rainfall in such a manner that halving the rainfall may be expected nearly to treble the value of the evaporation-rainfall ratio".

Another method of investigating rainfall variability is to deal with the months separately. In East African localities, however, the variability of several months in the year depends greatly on the annual variation in the dates the rainy seasons begin and end. This within wide limits is not likely to have an important biological effect, if the precipitation of the whole rainy season is not deficient, though the immediate effects on agriculture may be severe. Moreover, in low rainfall areas or in dry seasons of the year one brief storm may exaggerate single-month variability out of all proportion to its biological significance. On these general grounds it appears that an investigation of single-month variability is less likely to repay the labour involved than one of annual variability.

Variability in the nature of the rainfall is also of potential importance. As was found in South Africa by Schonken (1924), who incidentally makes a useful examination of the ideas implicit in the word "desiccation", a local rainfall may change significantly in its nature without a change in the annual total. Such a change may, through affecting the length of the influential rainfall period, alter the natural vegetation (Henrici, 1937); and if the individual storms become heavier the tendency is for a smaller proportion of the total fall to be utilizable by plants and for soil erosion to be favoured.

V. The nature and residual effect of the rainfall

Apart from its distribution through the year, a very important character of rainfall is the relative prevalence of light and heavy falls, a function of individual falls and their duration. Leake (1928), indeed, has remarked of the monsoon in India that the best agricultural result may be obtained from a definitely subnormal fall when this is well distributed. It will be obvious that the most beneficial rainfall is neither the very heavy, which may go to waste as "run-off", impoverishing the soil in the process, nor the very light, which may no more than damp the surface of the soil or may be intercepted.

The percentage of the rainfall intercepted and evaporated without reaching the soil may be surprisingly high and it varies greatly with the rate at which the rain falls. Herbaceous vegetation has been reported by Clark (1937) to intercept at least 50% of the rain when it is falling at the rate of about $\frac{1}{8}$ in. in the half hour, and at least 30% when the rain is falling twice as heavily. *Panicum virgatum*, a species comparable with much East African grass cover, intercepts, when its flower stalks are fully developed, 57, 67 and 81% of rain falling at the respective rates of $\frac{1}{2}$, $\frac{1}{4}$ and $\frac{1}{8}$ in. in the half hour. But

when such grass has been burnt, as happens frequently in East Africa, the soil receives for the time being, not a mere one or two-fifths of the recorded rainfall, but all of it. According to Geiger (1927), in coniferous forest, to which *Juniperus procera* stands are the East African equivalent, 20 % of the rain, however heavy it may be, fails to reach the ground; over 60 % of light falls (up to 5 mm.) are intercepted. Temperate broad-leaved canopies let through far more rain, over 50 % of even the lightest fall.[1] Freize (1936) finds in Brazilian primary forest, that while 67% of the year's rainfall is intercepted by the canopy, 60% ultimately reaches the forest floor.

To express the nature of the rainfall Walter (1910) proposed the "degree of wetness", a value to be determined for each month by the formula Rt'/t, where R = precipitation, t' = the number of days on which rain fell and t = the number of days in the month. Rainfall exceeding a daily total, selected arbitrarily by Walter, was regarded as wasted and excluded from account. Andrews (n.d., *ca.* 1923) utilized the same formula, deriving it indirectly from Walter. More recently Emberger (1932) advocated a similar formula, calculated on an annual basis. Neither Andrews nor Emberger attempted any correction for falls that were too heavy or too light to be proportionately effective.

Walter (1922) subsequently rejected his "degree of wetness" and attacked the problem of rainfall effectiveness experimentally by determining soil moisture losses in the top 30 cm. His data, obtained in Mauritius, showed incidentally that in a complete drought the loss of soil moisture was very slow indeed after about the first fifteen days and practically ceased after thirty. By means of the curve obtained from these data, and starting from a date on which saturation took place, Walter calculated the water loss on each day, and the balance, plus the recorded rainfall of that day, gave the effective soil moisture for the following one. A feature of this method is that all rainfall exceeding that required to saturate the soil is excluded from account, but all falls, however light, are credited as effective. It is not clear how this is to be reconciled with the Australian views (Section IIID), that falls below about 4 mm. (and more in a dry period) are ineffective, a conclusion likely to be applicable to East Africa.

Apparently in ignorance of Walter's work, Leake (1928*a*) developed a similar idea of "effective rainfall", defined as "a daily figure obtained by adding to the actual rainfall of any day nineteen-twentieths of the figure similarly obtained for the preceding day". Although the formula was evolved in India and was found to be of value in forecasting crops there, the rate at which it allows "effective rainfall" to diminish seems, from the East African point of view,

[1] Confirmation of this comes from an unexpected quarter. An Msambaa with whom I was walking in the local forest remarked that the *mwangati* (*Juniperus*) was well known to give a better shelter from rain than any other tree and that a piece of *Juniperus* was an essential item when making "medicine" to put an end to excessive rain.

unduly slow. A fall of 20 mm. would after 3 weeks unbroken drought still be nearly 7 mm. "effective". Hill (personal communication) found in Northern Nigeria that cotton wilted some considerable time before the theoretical depletion of the available moisture as calculated by Leake's formula. Moreover by this formula all rain, however light or however heavy, is similarly treated; thus a fall of 100 mm. in part of a day, which is by no means unusual in East Africa, would be credited as 95 mm. effective on the next day, a view hard to accept for most soils and surfaces by anyone who has had ocular evidence of the run-off that can take place. In fact, under certain conditions run-off may amount to no less than 90 % of the rainfall, a loss that can, by reafforestation and anti-erosion work, be reduced to one sixteenth (Gorrie, 1938).

Angström (1936), using Swedish data, has put forward a "coefficient of humidity" based on a function of the number of 100-minute units during which rain falls. He finds that the results run "closely parallel to the humidity factor of Martonne for monthly mean temperatures between 0° and 20° C." Although this coefficient is claimed in Angström's title as "of general applicability", it is based on the records of only a few Swedish stations at about the same altitude. The author himself thinks it probable that it does not hold good where "orographic influences" are operative. These are important in East Africa, and in any case the data for Angström's coefficient are only to be obtained by a multiplication of recording rain-gauges far beyond present resources.

The difficulties in the way of a satisfactory evaluation of "effective rainfall" over such an area as East Africa are, I fear, insuperable. One major difficulty will persist so long as the time unit of most meteorological records is the day, and a "rainy day" is one on which some rain, however little, falls. Another difficulty lies in the problem of the absolute limits of effective rainfall, a problem to which two groups of variables contribute. Of these the meteorological are by no means the more difficult to deal with; for "the infiltration capacity of soils is a complex property which varies not only between different soils, but also in the same soil with changing conditions within the soil" (Stauffer & Smith, 1937); and moreover, this inherent variability is overlaid with the variability, both in space and time, of the soil cover, by which, as indicated above, anything up to 80 % of the rainfall may be intercepted or, on the other hand, run-off may be more or less impeded. For these reasons it seems impossible that limiting values of effective rainfall can be found that are generally applicable.

VI. THE IMPORTANCE OF MIST AND CLOUD

A difficulty in classifying and mapping the climates of East Africa is the recognition that should be given to the prevalence of mist and cloud. They appear to be of great importance biologically in certain very localized areas;

but precise information about them is almost wholly lacking. Isonephs could certainly not be mapped. The mountain mists are characteristically developed in sharply defined belts, especially on isolated peaks and scarped plateaux. From personal experience I should say that the lower limit of mist prevalence tends to rise with distance from the sea, but that a constant level is soon attained. Thus, in the East Usambaras it may be placed at just below 4000 ft.; farther inland, as on the south face of Oldeani, at nearly 6000 ft.

Mist and cloud have a two-fold influence, first in shading (and here hot-season mist is of special importance) and second in providing what has usually been called "occult precipitation", but is perhaps better described as "horizontal precipitation" (Descombes, *cit.* Geiger, 1927). Two examples may be given of the shading effect. Swynnerton (1936) attributes to the prevailing cloudiness at Kikore (which is close to a scarp) the fact that the leaves of the savannah vegetation there were only beginning to turn yellow in July when thirty miles away much leaf fall had already taken place. Again, in the Veterinary Reserve at Mpwapwa, a clearing which is normally free of tsetse-flies, a very serious trypanomiasis infection of the experimental animals occurred during the months following the rains of 1937. This is attributed to the fact that, while as a rule high insolation confines the tsetses in the surrounding bush to the shade there, in 1937 the rains were followed by an unusual sequence of cloudy days which allowed the flies greater freedom of movement (personal communication by members of the Tanganyika Veterinary Department).

The influence of mist is shown most strikingly by the existence of a certain type of evergreen forest, appropriately called in German "Nebelwald", to which the "forêt de pluie fine" of Scaëtta apparently corresponds. Instrumental records of the meteorology of the Nebelwald areas are not abundant, but there is no doubt that these forests are capable of existing under a low rainfall. For example, at Shume, in the West Usambaras, the mean annual rainfall is below 800 mm. and the de Martonne index 33. The conclusion seems unescapable that the Nebelwald depends for its existence largely on the prevalent mist. Experiments on Table Mountain by Marloth appeared to show that the deposition there from mist might be sixteen times as great as the rainfall (Martin, n.d.). This result has been questioned, but from other work quoted by Geiger (1927) it does appear that in European forest total precipitation during mist periods may safely be taken at quite twice that recorded in the open close by. This conclusion is likely to be applicable with full force to the Nebelwald of East Africa, where the trees are often so heavily swathed with moss and beard lichen as to increase enormously the condensation area of each tree. In my experience this development reaches its maximum in a situation like that of the forest near the top of Longido, a sharp isolated mountain in dry steppe which has a de Martonne index under 20. Such forests as this should be regarded, I think, as persisting not so much because the existing conditions are favourable to forest growth as because their own nature and the

symbiotic relationship in which the trees are partners enable them to make an especially efficient use of the available moisture, and perhaps also because their existence helps to generate conditions to some extent favourable to them. When such forests are removed the vegetation that succeeds them, whether natural or crop, cannot form the same symbiotic relationship and must grow in a climate effectively less humid.

Those, then, are peculiar areas in which none of the classifications that have been proposed can do justice to the existing conditions; and it appears that on a climatic, no less than on a vegetational map, those areas would need to be specially indicated.

VII. Significant temperatures in East Africa

Climates have usually been described in terms of annual mean temperature, annual mean minima and annual mean maxima, a method that for the biologist is, beyond question, unsatisfactory. It is most difficult to imagine how an organism could respond to an annual mean temperature, and from the point of view of an organism, though not of logic, the annual mean maxima and minima represent even further abstractions. Extremely little seems to be known regarding what elements of natural temperature, e.g. minima, daily range or annual range, are likely to be limiting factors for animals, and particularly for vertebrates. Emberger (1932), Bowen (1933) and Moreau (1934) have suggested independently that the extremes, as expressed by the mean maxima of the hottest month and the mean minima of the coldest, are much more likely to be of biological significance and in any case they more accurately define any given climate than the means commonly quoted. Zotov (1938) concludes, for the vegetation of New Zealand, that summer temperature is the governing factor and he uses as criterion the mean temperature of the midsummer month.

However open to criticism the use of the annual mean temperature may be on theoretical grounds, it will obviously be a convenience in climatic classification if the extremes can be implied in a single figure. Mean annual temperature falls off with altitude at the rate of about 1·5° C. per 1000 ft. in East Africa; the mean annual minimum, however, falls off rather faster than the mean annual maximum, so that the range between these two means increases with altitude, as indicated in the B.E.A.M.S. chart reproduced by Moreau (1934). But on examining the available temperature records of a number of East African stations I find that the differences between the mean maxima of the hottest months and the mean minima of the coldest do not behave in the same way when arranged by altitude. Five stations on the sea-coast have an average range of 12° C. (the highest 13·1° C.) and six on, or in the immediate vicinity of, Lake Victoria (*ca.* 1100 m. or 3800 ft.) an average of 11·8° (with the

highest 14·0°). These two groups are sharply marked off from the following groups of "inland" stations:

(*a*) Six between sea-level and 1000 m. average 17·2° C.
(*b*) Eight between 1000 m. and 1200 m. average 17·0° C.
(*c*) Eleven between 1200 m. and 1500 m. average 17·7° C.
(*d*) Seven between 1500 m. and 2000 m. average 16·5° C.

Hence with the "inland" stations up to at least 2000 m. (6500 ft.), altitude does not cause any clear increase in the annual range as calculated from the mean maxima of the hottest month and the mean minima of the coldest. This range varies from 14° C. to nearly 21° in members of each of the four "inland" groups. Here high range in temperature might be expected to be correlated with bad distribution of rainfall, but it is not clearly so. The exact siting of the meteorological instruments, with particular reference to cold-air drainage, is probably a potent factor in the recorded ranges.

If, then, mean annual temperature is utilized for climatic classification in East Africa, it will be understood that in the immediate neighbourhood of the sea or of Lake Victoria it connotes an annual range of 12° C. ± 1·5°, and elsewhere a range of 17·5° ± 3·5°, irrespective of altitude.[1]

The relation between altitude and annual mean temperature is pretty constant throughout our area. On an unpublished chart supplied by the B.E.A.M.S. all the means of a variety of stations from 1° N. to 9° S. lie within 1·5° C. of the (straight-line) temperature-altitude gradient. No shift with latitude is perceptible. This is in the main confirmed by the gradients given for six Tropical Africa areas by Moreau (1934), but the latter shows that in abrupt mountains very close to the sea (Cameroons and Usambara) the temperature is lower, by about 3° C., than at corresponding altitudes elsewhere. To some extent this influence is felt farther inland. Walter (1937) has remarked that in Kenya "there is a distinct gradient between the west and east of the Rift Valley, the former being 2 to 3° F. [1 to 1·5° C.] higher in the mean than the latter". This difference is equivalent to that usually associated with a difference of 1000 ft. of altitude in the same locality. It appears, then, that a contour can within 500 ft. be taken as indicating the same annual mean temperature throughout East Africa, with the exception of the small Usambara plateau area, the only mountain country close to the sea.

The annual means referred to above are based on daily maximum and minimum temperatures. The relation between the mean so calculated and that obtained by integrating a thermograph record has been considered by Hartzell (1919). According to information supplied by the B.E.A.M.S. for four East

[1] Since the above was written Walter (1937, 1938) has stressed, with particular reference to crop-plants, the importance of daily range, interpreted in degree hours above and below critical temperatures. Localities near large bodies of water and in evergreen forest tend to form a group with daily range much lower than that of other localities; and at the same time there is a tendency for daily range to increase with altitude.

African First Order Stations, the mean calculated from the maximum and minimum is locally always too high, but by values only varying between 0·5 and 1·6° F., i.e. not exceeding 1° C.

The criteria of temperature appropriate to an East African climatic classification can now be discussed. Köppen (1936), as a result of a world-wide vegetational survey, specifies for his "Tropical Rain Climate" that no monthly mean should be less than 18° C. Throughout East Africa this boundary falls between the 1100 and 1400 m. contours. Bowen (1932, 1933) and Moreau (1935*a*) have found the most marked zoological transition to take place at about the level of the 21° isotherm, which in East Africa generally lies close to the 1200 m. contour, and hence may be taken as in fair agreement with Köppen's boundary.

After the Tropical Climate has been left behind there is an appreciable interval before typically Highland communities are met with: and the intermediate stage should perhaps receive formal recognition in classifying East Africa climatically. Köppen's subdivision of his Warm Temperate Climates is available, namely, his *Ca* and *Cb*, with warmest monthly means respectively above and below 22° C. I find on examination that in our area this boundary is connected with an annual mean of about 19° C. One distinction of Bowen's (1933) Highland Climate was that the mean maximum of the hottest month should be less than 80° F. (26·7° C.), which in East Africa occurs with annual means below about 18° C. Moreau (1934, 1936) found the Highland avifauna typically developed both in Usambara and on Kilimanjaro above the altitudes connoting the 18° C. annual mean. Lynes (1934) remarked in Iringa a faunal change between about 1800 and 1900 m., i.e. at about the 17° C. annual mean.

Thus the studies of Köppen, Bowen, Moreau and Lynes favour respectively the 19, 18, 18 and 17° C. isotherms as the lower limits of the Highland Climates. It appears then that the 18° isotherm may well be accepted; and for mapping this could be taken as the 6000 ft. or 1800 m. contour generally.

Chapin (1933) has observed that the line at which frost appears might be expected to prove an important ecological boundary. In fact it is, I think, far less important zoologically than botanically; but in any case it is a boundary impossible to determine with accuracy, or to generalize, because the incidence of frost depends so much on exceedingly local eco-climatic influences. By standard meteorological methods, i.e. in a screen, frost is practically never registered except above 2500 m. (say 8000 ft.), but appreciable, and even destructive, local ground frosts can appear at much lower altitudes. I conclude that the frost line cannot be used in classification in East Africa.

VIII. CONCLUSION

It does not appear that any one of the classifications reviewed in Section III can be adopted for East African purposes in its entirety. In general I think that too great hopes, which are illusory, have been placed on finding satisfactory

single-value factors, an opinion also held by de Philippis (1937). The factors proposed exhibit the most varied degrees of relationship to a reliable physical basis. In the main they have been concerned with attempts to evaluate "rainfall efficiency", as determined by the atmospheric factors contributing to evaporation, but some attention has been paid to "rainfall effectiveness", largely determined by the nature of the surface upon which the rain falls.

It appears to me that if classification were to be attempted under East African conditions nothing could be achieved without at least three distinct criteria, namely:

(*a*) Temperature.
(*b*) The duration of the rainy period of the year.
(*c*) The rainfall.

These criteria need to be discussed and definitions suggested.

(*a*) *Classification by temperature* (see Section VII)

The observed biotic transitions with altitude, the significant concomitant of which appears to be temperature, make it impossible to ignore this criterion in classification. In East Africa the upper limit of the Tropical Zone can, within 500 ft., be denoted by the 4000 ft. (1200 m.) contour, the lower limit of the Highland by the 6000 ft. (1800 m.) contour. The intervening 2000 ft. is classed as the Intermediate Zone. The outstanding exception to these generalizations is Usambara, where, owing to the peculiar topography, the boundaries are 1500 ft. lower.

It must, however, be stressed that we are still very ignorant of what elements of natural temperature are significant; for specific purposes some of them, e.g. minima or daily range, might have to be taken into account.

(*b*) *Classification by the duration of the annual rainy period* (see Section III D)

Since in different East African localities the period during which any appreciable rainfall may be expected varies from barely four months to fully eleven, it is obvious that this criterion must be of cardinal importance. Nevertheless, in certain circumstances its effect is masked. Highland evergreen forest exists in East Africa with an annual drought of four or five months, that is, under conditions much more rigorous than have been supposed by Köppen and others to be endurable by this vegetational formation. The explanation lies in the importance of "horizontal precipitation" within this type of forest (VI). This mitigant of the drought is, however, dependent for its continued potency on the maintenance of the forest. Generally, therefore, and on the long view, classification by duration of rainy period is not invalidated by this instance in which the expected effect of a restricted rainy period is counteracted.

Following Trumble, the rainy period may be called the "influential rainfall period", but in the absence of evaporation data it is impossible to calculate it

upon his basis. For the reasons given in (*c*) below it appears that the limit between a dry and a rainy month might be fixed in terms of recorded rainfall rather than of any function by which evaluation of rainfall efficiency is attempted. Different authors have used 20 mm. (Katanga), 25 mm. (India) and 50 mm. (Ruanda) as the limiting monthly rainfall. I suggest 40 mm., an admittedly arbitrary figure, for East Africa.

The "influential rainfall period" needs to be worked out from the weather of individual years, not from "normals", because the shift in the date of the "rains" from year to year tends to lengthen the rainy period appearing in the "normals". Also, the influential rainfall period, calculated on the monthly rainfall totals, will be on the average longer, probably by at least a fortnight, than the truth; because the first month ranking in that period in any one year often does so by virtue of rain beginning in its latter half, and in the last month of the period the rain often ceases after the first few days. It not infrequently happens that a single month in which the rainfall is a few millimetres above the influential threshold occurs between two or three definitely dry months. In these circumstances the odd month must be regarded as part of the dry sequence; but over a large part of East Africa two well-defined influential rainfall periods in the year must be recognized.

(*c*) *Classification by the rainfall*

Implicit in the recognition of an influential rainfall period is the rejection, as not significant, of the rain that falls outside that period; so that this third criterion must be based on the rainfall of only the influential period (or periods).

Nearly all classifications have preferred to use, not recorded rainfall, but some single-value factor designed to evaluate rainfall efficiency. The factors that have a respectable physical basis cannot be used in East Africa for lack of evaporation data. The alternatives that have been suggested are functions of rainfall and temperature (III B). But, especially in East Africa, wind and relative humidity, of both of which we have altogether too few records, are potentially more important than temperature in determining evaporation. Therefore, if we seek to evaluate rainfall efficiency as a function of temperature we are laying all the emphasis on a variable that is less significant than two variables that are left out of account. Moreover, the mean or the minimum temperatures, which have been the values utilized in the rainfall efficiency functions proposed by various authors, are of little relevance without knowledge, which we lack, of the course of the relative humidity and hence of the dew-point.

From the foregoing I conclude that any evaluation of rainfall efficiency would have to be made by means of some function open to such grave objection that the operation could not be justified. As the basis of classification, the recorded precipitation is preferable, as likely to be, at the worst, no more unsound than any adjustment of it we can make.

However acceptable such a scheme of classification might appear, several considerations detract from its local and practical value, namely:

(i) The second and third criteria are based on averages; but the extremes, especially the low-rainfall extremes, are of great importance in delimiting biotic potentialities (IV).

(ii) Because it can take no account of mist and cloud, the classification would give no clue to the areas in which the drier communities of that specialized and scientifically important biome, the Highland Evergreen, may be expected.

(iii) This classification (like others) takes no account of the "effectiveness" of the recorded rainfall, depending on the nature of individual falls and the soil-moisture relations. Especially on account of the local variation of this latter factor, and its rapid variability in time, there is no prospect of giving due weight to "effectiveness".

Finally, to the mapping of climates on this, or any other, classification, East African physiography opposes a grave difficulty. Meteorological stations are in wide areas still so sparse that climatic boundaries could only be drawn conjecturally; and from this point of view any reasonably acceptable climatic map must be on a small scale, less, I should say, than 1 : 2 million. On the other hand, such a map could not do justice to the abrupt local transitions, which are among the best authenticated and biologically important climatic features.

IX. Summary

The extent of the available meteorological data for East Africa is indicated. Such maps of the East African climates as exist, mostly incidental to world-maps, are incomplete or inaccurate; in none of them is climate related to relief, which is so important a determinant.

The numerous climatic classifications that have been proposed are reviewed. They exhibit a most varied degree of complication and, where single-value factors are advocated, of relationship to a physical basis. All are based on "normals", taking no account of extremes, the importance of which must be stressed.

The single-value factors with a respectable physical basis are functions of rainfall and evaporation, but they cannot be used in East Africa for lack of data. In default, the best classification might be by three criteria: (*a*) temperature, (*b*) length of influential rainfall period, (*c*) recorded rainfall of that period. But this must be expected to be locally unsatisfactory because it does not take into account (i) climatic extremes, (ii) "horizontal precipitation", which appears to be crucial for the existence of much evergreen forest, (iii) "rainfall effectiveness", depending on the intensity of the rainfall and on the nature of the soil.

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REVIEWS

THE JOURNAL OF ANIMAL ECOLOGY

VOL. 7, NO. 1, MAY, 1938

THIS number (198 pages) contains eleven original papers dealing with research in Great Britain, Iceland, Svalbard, West Greenland and Ceylon; also nine reviews, 142 Notices of Publications on Animal Ecology, together with the business reports and list of members of the British Ecological Society.

There are three important ecological surveys done in Great Britain: terrestrial, freshwater, and marine. Miss Enid Nelmes gives the results of a very thorough investigation of the distribution in Great Britain of the wood ant (*Formica rufa*), a species which lends itself to exact mapping owing to the comparatively permanent nature of its colonies. The distribution map for England is superimposed on a geological and soil map assembled from various scattered sources. There is a marked correlation between the ant colonies and certain soils, especially sand, and a general tendency to avoid calcareous and clay soils. T. T. Macan has surveyed the distribution within the English Lake District of the Corixidae, a group of freshwater Hemiptera known as the "lesser water-boatmen". The species are distributed in groups which follow the succession stages of vegetation in different bodies of water, in particular the succession from low organic content to high organic content of the soils. He also distinguishes a special group of species in high tarns. A. Laurence Wells describes the Thames estuarine plankton, including both phyto- and zooplankton, chiefly on the basis of collections taken at Southend-on-Sea. The seasonal changes in diatom and Copepod species are defined, and many valuable biological notes on other groups are included. This Thames plankton is the support of various cockle, oyster, shrimp and whitebait fisheries.

Two surveys were done in the Arctic. G. C. L. Bertram and David Lack greatly extend previous knowledge of the animal communities of Bear Island (an island in Svalbard, lying between Norway and Spitsbergen). Their account of the fauna is derived from a 7½ weeks' survey in 1932. They explored new ways of describing the animal communities without defining their distribution solely by the plant associations. In particular the importance of humidity to Collembola and Acarina is stressed. The observations on the fauna inhabiting the richer vegetation of bird cliffs are specially interesting, also records of great individual abundance of some species. In a lengthy discussion of the origin of the fauna the authors conclude that there has been no post-glacial land bridge, that the fauna has reached the island by aerial or drift-ice dispersal, and that colonization is still continuing.

David Stevens records, by means of quantitative population records, the four types of intertidal shore fauna at Amerdloq Fjord in West Greenland. These comprise, rock, sand, stream mouth and *Mytilus* beds. He also discusses the validity of various geographical "zones" for marine animals that have been proposed. A. C. Stephen has an account of another marine intertidal community, that inhabited by the bivalves *Tellina tenuis* and *fabula* in the Clyde Basin in west Scotland. Annual counts of sample populations disclosed a fluctuation in the number of young establishing, with peaks ("good spat years") every three or four years. These are explained by a provisional correlation with fluctuations in water temperature. A. C. Stephen also records in another paper some of the unusual marine visitors to British shores during the unusually warm-water years of 1932–4.

Other papers are: a parasite survey of Ceylon rats, assembled by Gordon B. Thompson; an account of the wild field mouse (*Apodemus*) inhabiting birch scrub in Iceland, by Miss

Patricia Lupton and Miss Ursula Wykes; and notes on the house mouse (*Mus musculus*) and a census of breeding birds on the Isle of May, Firth of Forth, by H. N. Southern.

There are reviews of the *Journal of Ecology*, and of publications on the philosophy of ecology, North American mammal ecology and bird populations, the Little Owl Food Enquiry, British dragonflies; and of the new edition of Shelford's "Animal communities in Temperate America, as illustrated in the Chicago Region."

The Notices of Publications on Animal Ecology are, as usual, issued in a reprinted duplicate with the *Journal*, and can also be bought independently for a small sum. An innovation is that they are now re-issued in stiff covers, with cut-down margins, in order that people who may not be able to take the *Journal* itself, can keep in touch with the literature on British animal ecology, retaining the booklet as a record or cutting out certain references for card-indexing if desired.

CHARLES ELTON.

BRITISH EMPIRE VEGETATION

Adamson, R. S. *The Vegetation of South Africa.* Pp. xvi + 235, with 23 figures and 12 maps in the text, and 17 photographs of vegetation. London: British Empire Vegetation Committee. 1938. Price 10*s.* post free. (Obtainable from: The Registrar, The University, Cape Town; The Chief of the Division of Plant Industry, Pretoria, Transvaal; and The Assistant Director, Royal Botanic Gardens, Kew, England.)

This monograph merits particular notice because it is the first of a series on the vegetation of different regions within the British Empire. It is a result of the work of the British Empire Vegetation Committee and as further publications of a similar type are dependent upon the financial success of the earlier ones, it is especially to be hoped that botanists in general will give adequate support to the venture.

The book itself needs no artificial aids to appreciation. It is a good deal more than a botanical treatise. It is also a guide to the natural resources of the Union of South Africa, indicating as it does the inter-relations between geology, soils, climate, vegetation and modes of exploitation. From this wider point of view the treatment is largely coloured by the idea, expressed by Prof. A. G. Tansley, that proper exploitation can only be planned in the light of a knowledge of what nature does when left to itself.

From the ecological point of view, Prof. Adamson draws a picture of vegetation types developed for the most part under climatic conditions in which evaporation is greatly in excess of precipitation. The resultant aridity increases in passing from south-east to north-west, and vegetation along the same axis tends to change from types in which trees predominate towards bushy grasslands and finally semi-deserts. Prof. Adamson is at pains to disarm local critics by disclaiming any intention of discussing local variations and by confining himself to the main features of the vegetation. Certainly he has succeeded in presenting a concise and easily intelligible account of South African vegetation as a whole, while at the same time he does adequate justice to those features, particularly of the Cape flora, which are possibly more widely known.

The predominance of bush-savanna types in South Africa is, of course, one of the interesting features of the country. In regard to these, current descriptions of African savanna types often leave the feeling that many of the types included under this heading are of biotic origin, greatly affected by grazing and burning, and not properly to be included as climatic climax types of vegetation. Prof. Adamson's account is, however, free from ambiguity in

this respect and it certainly conveys the impression that a high degree of continuity of cover by the tree or bush layer is a feature characteristic of the natural climax vegetations.

The importance of grasses as constituents of South African vegetation lends particular point to the frequent indications of the operation of the grazing factor. The view is accepted, that the effect of European colonization has resulted in increase in grazing pressure, even though the enormous herds of wild grazing animals formerly existing have now been nearly destroyed. Formerly these animals spread widely in the wet seasons and only frequented the moister areas in the dry season, whereas now, the effects of domesticated grazing animals are localized and a high grazing pressure on the moister areas may be maintained continuously. This has disastrous effects on the natural vegetation and in extreme cases grasses may be completely suppressed, and the area may be entirely occupied by plants which are not eaten by animals. Thus *Helichrysum argyrophyllum*, a prostrate undershrub with white woolly leaves, may, to the exclusion of grasses, become completely dominant on overgrazed areas in savanna. Even in grassland areas, bushes may entirely replace the grasses under conditions of overgrazing. The effects of the destruction of the natural vegetation cover upon soil erosion are as well marked in South Africa as they are in other areas of a similar climatic type.

In view of the modern tendency to relate both soil and vegetation to climate as well as to one another, the author's descriptions of South African soil types are of great interest, although the available information is not exhaustive and it appears that in this instance the ecologist may be ahead of the pedologist. South Africa appears on the whole to possess a large proportion of shallow and immature soils, and also, on account of the scarcity of limestone, some of quite especial interest. Thus, although in view of the climate many of the grassland soils might be expected to belong to the Tschernozem group of the northern hemisphere, the general scarcity of lime makes it difficult to distinguish any lime accumulation, while in colour and in other features the profiles are very distinctive. It seems probable, in short, that the peculiarities of some of the South African soils may involve a revision of the existing classification of soil types.

The relation between climate and vegetation has thus to centre mainly around fluctuations in temperature and humidity, although complications due to varying podsolization of the soil are observed in the vicinity of the Cape. Prof. Adamson emphasizes the importance of frosts as factors tending to delimit certain vegetation types, particularly forest as contrasted with savanna and grassland types, and also makes pertinent observations on the importance of variability of rainfall. Enough, however, has already been said in this brief sketch to show that this is a book of great utility and very considerable interest.

W. H. P.

Davy, J. Burtt. *The Classification of Tropical Woody Vegetation Types.* Pp. v + 86. Oxford: Imperial Forestry Institute, Paper No. 13. Price 2*s.* 6*d.*

While the subject of this paper is designed primarily for use in the British Empire it is not strictly speaking limited to it. The paper is an enlarged and revised summary of one discussed at the last meeting of the British Ecological Society. In it, Dr Davy trys to find common ground for the classification of tropical woody vegetations. He first summarizes the classifications of Schimper, Warming, Chipp and Champion, and then suggests a general basis of classification, with appropriate names for each of the vegetation types distinguished. Apart from the value of this general summary the paper has the merit of presenting the information in a form suitable not only for the use of professed ecologists but also for forest officers for whom it is specially designed. The standardization of the nomenclature alone will, of course, be a great help in this direction. In addition, however, there are explanatory remarks, a glossary of the ecological terms employed, a list of papers giving further details

and, finally, a long and very useful series of suggestions as to the sorts of detailed observations that may profitably be made in the field.

The essence of the classification employed appears to be the separation from the group of woodland vegetation types, of forests with a closed assemblage of trees and a continuous canopy. This permits of a varied treatment of savanna types though logically it may suggest that difficulties may arise in definition in handling such units as "thorn-forest". The implications of the text are, however, clearly that Dr Davy would prefer a general agreement as to what is to be classified and what names are to be used rather than a purely logical classification. It is much to be hoped that this paper will further this ideal. W. H. P.

ECOLOGY IN THE UNITED STATES

Weaver, J. E. & Clements, F. E. *Plant Ecology.* Pp. xxii + 601, 1 coloured map and 271 illustrations. London: McGraw-Hill. Price 30*s*.

This is the second and much enlarged edition of a book which was first published nearly ten years ago. It is both a textbook and a work of reference and in both capacities the main test which should be applied to it is that of its utility. Both of its authors are experienced ecologists and teachers, and, in addition to a wide survey of general ecological problems, they have given considerable attention to the question of supplying an adequate practical background to the material incorporated. The examples indicated appear to be as suitable in Europe as in America and the wide and increased range of the work is possibly indicated by the fact that over one thousand references are now cited. There is no doubt that the book will serve its intended purpose and that it may be recommended both as a text and as a reference volume worthy of its authors.

Apart from this role, the book is of interest in the indication it gives as to the directions in which ecological achievement has progressed in the last ten years. Perhaps foremost in the list of changes should come the difference in outlook towards xerophytes and with it a much clearer understanding of the effects of habitat factors upon the water relations of plants. Another direction in which change has been pronounced is in the development of the idea that climate determines soil development and so, in this way also, affects the vegetation. Lastly, comes an increased realization of the importance of vegetation cover in problems of conservation, both of water supply and against soil erosion. In this field, so much work has been done in the U.S.A. that the extensive consideration given to these and allied problems is very timely. Further, the prominence given to topics of this type and to various aspects of crop ecology is quite characteristic of the difference in outlook between the contents of this book and the views and work of many European plant ecologists. Such additional features as the detailed study of root systems, the use of phytometer methods and the emphasis laid on plants as indicators, not only reflect the special knowledge acquired by the authors in their detailed studies, but also suggest reasons why the book should be stimulating to European ecologists. Finally, the fact that both authors have had much to do with ecological work in the "continental" areas of North America, and in areas where water plays a preponderant part as a habitat factor, tends to make the volume of equal value to botanists whose interests centre in arid areas. W. H. P.

Carpenter, J. R. *An Ecological Glossary.* Pp. ix + 306, with 12 appendices including 6 maps. Norman, Oklahama: University of Oklahama Press. Price $4.00.

This is not perhaps a work of which it is possible to write an extensive review, but it is certainly a book worthy of notice as an attempt to solve a problem which is becoming

increasingly severe, that of bringing into line the multiplicity of meanings which is affecting ecological nomenclature. By bringing together the refinements which have modified the original meanings of many of the commoner terms and by bringing existing terminology into one place, the author hopes to prevent or at least to help to prevent, the excessive duplication of names which is likely to take place in a subject undergoing rapid development. He points out in particular that animal and bio-ecologists will otherwise tend to create terms for things or concepts which may already have been defined by plant ecologists. It is clear that there is a definite place in ecology for a book of this type. Its value to the general and non-ecological reader is obvious.

The scope of the book is indicated by the fact that it includes nearly 3000 definitions, a list of useful sources and reference papers, and finally appendices dealing with equivalent terms in use by different schools of plant ecologists and including maps and tables of life zones and of biotic areas.

W. H. P.

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